Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE
Vol. 106, No. 1

AMPHISBAENA FULIGINOSA

Contributions to the knowledge of the Brasilian lizards of the family *Amphisbaenidae* Gray, 1825. 6. On the geographical distribution and differentiation of *Amphisbaena fuliginosa* Linné.

By P. E. Vanzolini

From the Departamento de Zoologia, S. Paulo, Brasil.

With Two Plates

CAMBRIDGE, MASS., U. S. A.
PRINTED FOR THE MUSEUM

April, 1951

No. 1 — *Amphisbaena Fuliginosa*

By P. E. Vanzolini

INTRODUCTION

The herpetofauna of South America is a very good subject for the study of comparative evolution. Among the circumstances that favor this study are: the heterogeneity of age and origin of the major groups, the diversity of types of environment, the large ranges of many species and the relatively simple geological history of the continent. The South American herpetofauna presents a wealth of evolutionary situations, without the accompanying problems of paleogeography and migration that obscure the phenomena of speciation in other regions, as, for instance, the West Indies.

It is true that an extremely large amount of cataloguing work remains to be done and a still larger amount of very poor taxonomic work to be done over. It is also true that there are practically no collections from considerable portions of the continent.

In some cases, however, the taxonomic situation is clear enough and the number of available specimens warrants an investigation of the features of speciation and even of evolution on the generic level.

Those studies, in my opinion, should be as thorough as possible, presenting not only the conclusions reached but also the complete factual basis for them. I have been told that simple presentation of the results, in the form of a new (or confirmation of a previous) taxonomic situation, is all that is to be desired. This has been the general attitude of the herpetologists working with South American material. They have been on the whole more concerned with the demonstration of the existence of differentiation, and the consequent assignment of subspecific names, than with the establishment of more detailed patterns of variation. It is my belief, however, that only by the accumulation of a very large body of exact information shall we be able to prepare the field for a new work of synthesis, to succeed those of Rensch, Mayr, Huxley and others, that are today an obligatory part of the background of the modern systematist.

In the course of a revision of the Brasilian species of *Amphisbaena* I realized that Amphisbaena fuliginosa would be a desirable subject for a study as delineated above. Besides the evolutionary interest of such a study, it is always useful during the preparation of a revision to make a careful study of variation of the most abundant species, in order to have a sounder basis to extrapolate when dealing with rare forms. I was able to secure 129 specimens of *A. fuliginosa*, representing

58 localities. This is the largest number of New World amphisbaenians of one species ever assembled. Although in some cases fragmentary and insufficient, the material in my hands enabled me to attempt a statistical analysis of the problems of geographical variation and of variability within homogeneous samples of *A. fuliginosa*.

In this statistical analysis I endeavored to use the largest possible number of characters. Seven of them were finally selected: (1) number of body annuli; (2) number of tail annuli; (3), (4) number of segments (dorsal and ventral) on a midbody annulus; (5) number of preanal pores; (6) relative tail length and (7) color.

Other characters usually employed in saurian systematics were found to be unsatisfactory in the case of *A. fuliginosa*. The head shields, for example, present in this species an enormous amount of individual variation; in many cases there were important differences between the right and the left side of the same specimen. Preliminary analysis showed that intra-sample was as large as inter-sample variation and so this whole set of characters was abandoned.

The relative length of the head presented another problem that could not be solved, since there were no satisfactory points of reference for measurement.

Finally, osteological characters show no significant geographical variation in the small series of skulls available and need not be mentioned here.

The problem of geographical differentiation in *A. fuliginosa* has been attacked in two steps.

The first approach has been the investigation of the existence and features of differentiation for each character studied. This has been done chiefly by means of statistical tests for homogeneity and differences between samples from neighboring localities.

All the characters investigated showed geographical differentiation. No case of perfect parallelism between two characters was found. And, in all cases where suitable material was available, intergradation between adjacent samples was detected.

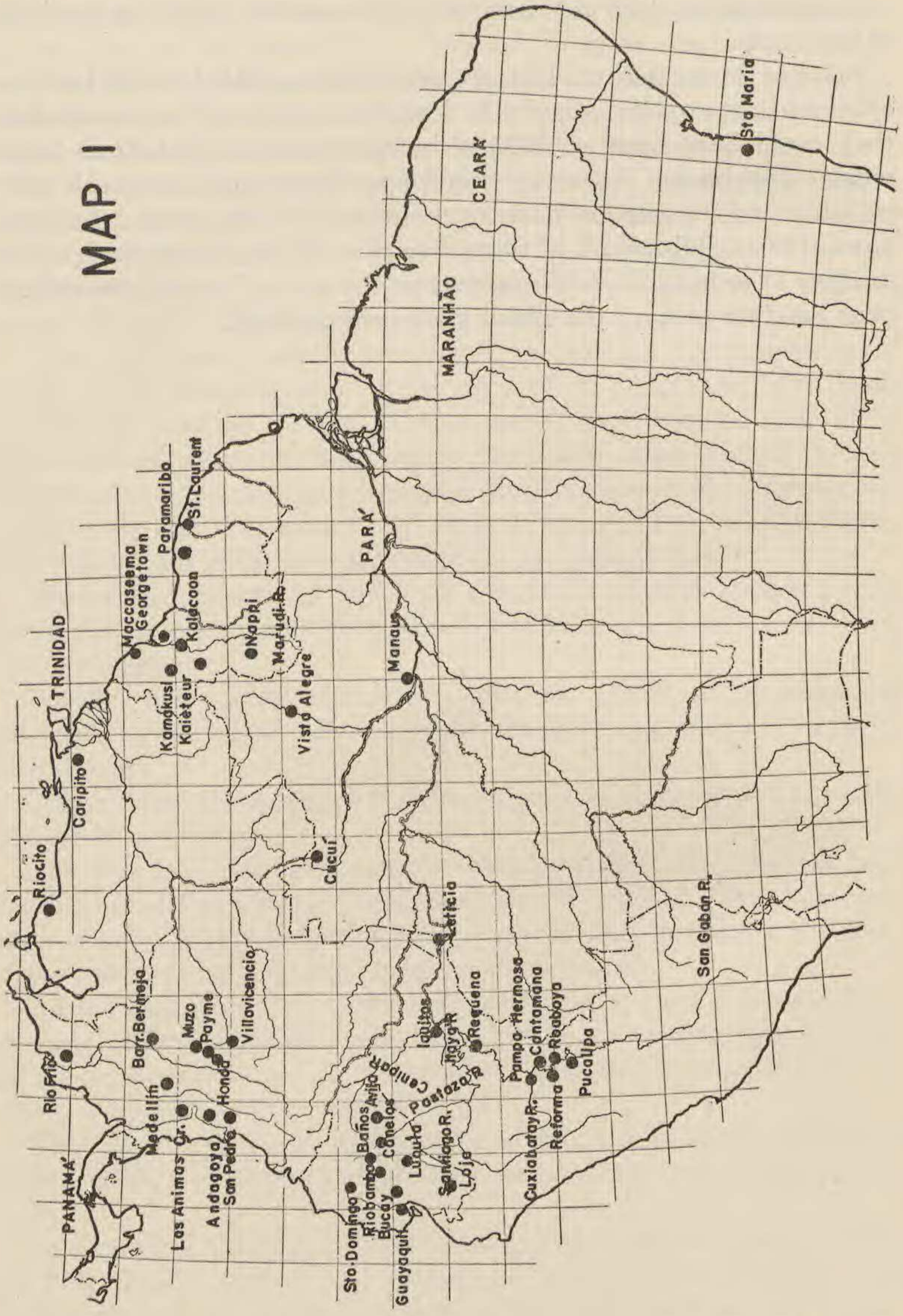
The second step was to assemble these data and to study differences between the several pairs of samples, using all the information available.

As a result of this phase of the investigation it became apparent that no two samples agree in the totality of the characters studied. The broad pattern of variation seems to be of a "checkerboard" type. Some elements, however, lead to the belief that this picture conceals one of adaptive differentiation following expansion of range.

Finally, as a taxonomic result, five subspecies are considered as distinguishable at present; for two of them old names are available; three require new names.

A question has been put to me as to the need for statistical methods in this study.

I do not doubt that the five subspecies here established can be identified without any statistical aid. I am even prepared to concede that they could have been established independently of statistical treatment. This course, however, would have been open to considerable criticism and I would not have any confidence in the results. Furthermore, the establishment of those five races is but a corollary of the analysis of geographical differentiation; this analysis would never have been possible without the use of statistical methods.



MAP I

Map 1. Localities from which material has been available for this study. No great attempt at precision has been made. Localities omitted: *Cashiboya*, overlaps the mid-Ucayali cluster of localities (Contamana, etc.); *Peña Lisa*, overlaps *Andagoya*; *Aventino*, not located.

TABLE 1

A. fuliginosa — Material used in this study

Locality	*Collection and Number*	*Sex*	*Length*[1]	*Annuli*[2]	*Segm.*[3]	*Pores*
BRASIL						
Manaus, Amazonas	AMNH 64917	♂	152+x	210+x	24/22	8
" "	AMNH 64918	♀	170+21	207+25	22/22	8
" "	AMNH 64919	♀	280+37	211+24	24/24	8
" "	IB 673	♀	260+33	212+25	24/24	8
" "	IB 674	♀	240+30	214+26	24/24	8
" "	DZ 1927	♀	290+40	219+26	26/24	9
" "	MCZ 19540	♂	230+29	220+24	24/24	8
" "	MCZ 20663	♂	270+39	215+26	26/24	8
" "	MCZ 20664	♀	330+40	212+25	22/26	8
" "	MCZ 20665	♂	170+25	220+28	24/24	8
Cucuí, "	AMNH 37442	♂	390+x	208+x	22/22	8
" "	AMNH 37443	♂	205+32	214+29	20/22	8
" "	AMNH 37444	♂	260+x	205+x	22/20	6
Vista Alegre, Amazonas	MCZ 20649	♂	285+41	202+25	22/24	8
—, Pará	USNM 7364	♀	260+x	202+x	26/28	8
—, Maranhão	MCZ 5747	♀	345+x	208+x	24/22	8
—, Ceará	IB 681 A	♂	x+x	214+24	22/24	8
—, "	IB 681 B	♀	250+30	214+25	24/24	10
—, "	IB 681 C	♂	260+40	203+27	20/20	8
Santa Maria, Baía	AMNH 1091	♀	335+51	206+24	26/26	9
" " "	AMNH 1092	♂	280+49	197+28	26/26	10
" " "	AMNH 1093	♂	250+x	202+x	26/24	8
PERU						
Iquitos, Loreto	CM 45471	♀	341+x	213+x	22/22	8
" "	CM 45472	♂	270+40	208+26	24/22	6
" "	AMNH 56224	♂	250+x	208+26	22/22	8
" "	AMNH 56588	♀	450+75	206+27	22/22	8
" "	AMNH 56589	♀	280+47	209+28	22/22	8
" "	AMNH 56590	♂	270+46	205+29	20/24	8
" "	AMNH 56592	♀	330+x	204+x	22/20	8
" "	AMNH 56596	♀	365+64	206+29	22/22	8
" "	AMNH 56597	♂	360+61	211+30	22/22	8
" "	AMNH 56598	♀	305+55	209+29	22/22	8
" "	AMNH 56599	♂	255+52	210+29	22/22	8
" "	AMNH 56600	♀	275+51	210+30	22/22	8
" "	AMNH 56602	♀	300+50	204+28	20/22	8
" "	AMNH 56603	♂	245+39	207+27	22/22	8
" "	AMNH 56605	♀	340+57	205+29	22/22	8
" "	AMNH 56610	♂	395+75	208+29	22/22	8
" "	AMNH 56617	♀	370+60	206+29	22/22	8
" "	AMNH 56618	♀	360+61	210+30	22/22	8

TABLE 1 — (*Continued*)

Locality	*Collection and Number*	*Sex*	*Length*[1]	*Annuli*[2]	*Segm.*[3]	*Pores*
Contamana, Loreto	AMNH 56594	♂	105+16	210+26	20/18	8
" "	AMNH 56609	♀	295+50	208+29	22/22	8
Pampa Hermosa, Loreto	AMNH 56310	♀	365+62	208+28	22/22	8
Cuxiabatay R., "	AMNH 56611	♀	305+46	211+27	22/22	8
Roaboya, Loreto	AMNH 56606	♂	275+42	209+28	20/22	7
" "	AMNH 56607	♂	275+45	211+28	22/20	7
" "	AMNH 56613	♂	245+39	212+26	20/22	7
Requena, "	AMNH 56608	♂	205+35	215+29	22/20	8
Reforma, "	AMNH 56601	♀	315+56	204+29	22/22	8
Pucallpa, "	MCZ 45784	♀	325+48	215+29	20/18	8
Cenipa R., "	AMNH 56593	♀	315+x	196+x	20/22	8
" "	AMNH 56595	♂	290+x	219+x	22/22	7
ECUADOR						
Avila, Napo-Pastaza	SU 8259	♀	365+60	200+26	20/22	8
Pastaza R., Napo-Pastaza	MCZ 37271	♂	370+x	207+x	x x	x
Luoula (Upano R.), Santiago-Zamora	AMNH 28784	♀	380+64	202+27	22/22	9
Luoula (Upano R.), Santiago-Zamora	AMNH 28785	♀	350+x	200+x	20/22	8
mouth of Santiago R., Santiago-Zamora	AMNH 56612	♀	300+55	205+28	20/22	8
between Baños and Canelos, Santiago-Zamora	AMNH 37862	♀	200+x	205+x	22/22	9
Riobamba, Chimborazo	AMNH 2285	♀	340+x	197+x	22/22	8
" "	AMNH 23324	♀	275+44	204+26	22/22	8
" "	AMNH 23325	♂	360+62	203+29	22/22	8
" "	AMNH 23326	♀	295+45	202+26	20/22	8
" "	MCZ 7799 A	♂	345+50	199+23	22/22	8
" "	MCZ 7799 B	♀	320+46	205+25	22/24	7
Bucay, Guaymas	AMNH 22090	♂	350+55	198+25	22/22	7
Daule R., "	MCZ 3572	♀	220+34	196+27	24/20	8
COLOMBIA						
Leticia, Amazonas	MCZ 48959	♀	340+x	214+x	20/22	8
" "	MCZ 48960	♀	250+40	221+26	26/24	10
" "	MCZ 48961	♂	255+39	207+25	24/24	8
Villavicencio, Meta	CM 30583	♀	235+38	208+26	24/24	8
" "	AMNH 62137	♀	440+x	206+x	24/26	8
" "	SU 8272	♂	400+55	207+25	26/26	9
" "	SU 8273	♂	190+30	199+25	24/26	8
Paime, Cundinamarca	MCZ 17647	♀	290+45	196+24	22/20	x

TABLE 1 — (*Continued*)

Locality	*Collection and Number*	*Sex*	*Length*[1]	*Annuli*[2]	*Segm.*[3]	*Pores*
Honda, Boyacá	AMNH 27495	♂	285+45	201+25	22/24	8
" "	AMNH 37455	♀	315+50	205+26	26/24	8
Muzo, "	AMNH 27496	♀	310+45	196+24	22/22	7
" "	MCZ 42189	♀	265+38	290+23	22/20	6
" "	MCZ 46437	♂	250+34	197+24	20/22	6
Medellin, Antioquia	AMNH 37440	♀	280+x	196+x	20/20	6
" "	AMNH 37441	♂	115+19	195+25	24/24	7
Barranca Bermeja, Santander	CM 27575	♂	225+35	200+27	20/22	8
Las Animas Creek, Quito R., Chocó	AMNH 18237	♂	315+47	192+25	24/24	8
Andagoya, Chocó	MCZ 29683	♀	405+58	194+24	22/20	6
San Pedro, Valle del Cauca	AMNH 37439	♀	285+40	201+24	22/24	6
Rio Frio, Magdalena	MCZ 25052	♀	320+50	199+25	22/20	7
VENEZUELA						
Riocito (Acosta), Falcon	MCZ 49049	♀	260+39	200+26	24/26	8
PANAMA						
Panama City	MCZ 37874	♂	240+36	195+24	22/22	8
" "	MCZ 37123	♀	295+x	200+x	24/22	8
Frijoles, Canal Zone	MCZ 24003	♀	240+x	200+x	22/24	8
Barro Colorado Id., Canal Zone	MCZ 22070	♂	315+46	197+24	22/22	8
Monte Lirio, Canal Zone	MCZ 18925	♀	315+x	200+x	22/22	8
" " " "	MCZ 24004	♂	285+42	196+23	24/24	9
near Gatun	MCZ 18924	♂	280+41	195+27	22/22	8
midbasin Chagres R. and Pequeni R.	MCZ 37106	♂	330+x	202+x	24/22	8
Chagres R. (Bohio)	USNM 38399	♂	350+52	198+24	24/24	8
Canal Zone	USNM 37859	♀	305+x	201+x	24/24	8
BRITISH GUIANA						
Marudi R.	AMNH 60907	♀	230+32	218+29	24/22	8
Kaieteur Falls	AMNH 1085	♂	195+29	199+25	22/22	8
Kamakusi	AMNH 25088	♀	205+x	204+x	20/20	8
Kalacoon	AMNH 8731	♀	250+39	205+26	22/22	9
Georgetown	AMNH 17689	♀	420+55	213+24	24/24	8
"	AMNH 7295	♀	305+39	207+24	22/24	9
"	AMNH 17688	♂	230+31	208+25	22/24	8

TABLE 1 — (*Continued*)

Locality	*Collection and Number*	*Sex*	*Length*[1]	*Annuli*[2]	*Segm.*[3]	*Pores*
DUTCH GUIANA						
Paramaribo	AMNH 8134	♀	240+36	207+26	24/22	9
"	AMNH 8135	♀	285+x	206+x	26/26	8
"	AMNH 8140	♀	145+22	205+25	26/22	8
"	AMNH 8649	♂	215+x	196+x	24/24	10
"	AMNH 8650	♂	275+39	206+25	26/24	8
"	AMNH 8678	♀	135+21	199+27	24/22	8
Surinam	USNM 6118	♀	370+x	205+x	28/24	8
"	USNM 58739	♂	225+38	203+27	28/26	9
"	MCZ 15719	♂	350+51	216+25	22/24	8
TRINIDAD						
Toco	MCZ 10137	♀	310+x	205+25	22/22	6
Brackfield	CM 49910	♂	240+37	207+27	22/22	8
San Rafael	CM 49911	♂	245+39	206+24	24/20	8
" "	CM 49912	♀	280+42	206+26	22/24	8
" "	CM 49913	x	x+x	205+x	x x	8
Caparu	AMNH 6968	♀	260+42	206+26	22/24	8
Tucker Valley	AMNH 64440	♂	265+40	211+26	22/24	8
" "	AMNH 64462	♀	215+30	205+24	20/22	8
" "	AMNH 64462 A	♂	250+38	210+25	20/24	7
" "	AMNH 64462 B	♀	210+29	212+25	20/22	6
" "	AMNH 64462 C	♀	195+25	203+24	22/24	6
" "	AMNH 64523	♀	250+x	204+x	20/22	7
" "	AMNH 64523 A	♂	200+26	209+27	20/20	6
" "	AMNH 64523 B	♂	235+36	204+27	20/22	6
— —	USNM 5751 A	♂	262+41	202+25	22/24	6
— —	USNM 5751 B	♂	210+26	205+26	24/26	8

---

[1] Snout to vent length plus tail length.

[2] Number of body annuli plus number of tail annuli.

[3] Number of dorsal segments / number of ventral segments to a midbody annulus.

TABLE 1A

A. fuliginosa — Material arrived too late for statistical analysis

Locality	*Collection and Number*	*Sex*	*Length*	*Annuli*	*Segm.*	*Pores*
PERU						
Rio San Gaban, Loreto	BM 703		275+40	207+27	20/20	8
" " " "	BM 740		275+41	207+27	20/20	7
" " " "	BM 744		335+53	205+27	22/20	7
Cashiboya, "	BM 704		270+x	210+x	20/20	8
ECUADOR						
Santo Domingo	BM 742		295+42	193+23	22/24	8
Guayaquil, Guaymas	BM 741		315+51	200+28	22/22	9
50 km E Loja, Zamora	BM 745		275+41	199+29	20/22	8
COLOMBIA						
Peña Lisa (Condoto), Chocó	BM 714		325+45	202+24	22/24	7
VENEZUELA						
Aventino (not located)	BM 700		310+51	204+28	24/26	8
Caripito	AMNH 69729	♀	260+40	209+27	24/24	6
"	AMNH 69728	♂	175+26	206+28	24/22	6
BRITISH GUIANA						
Maccaseema	BM 747		180+x	205+25	24/26	10
"	BM 748		235+35	207+24	24/26	8
Nappi, Kanuku Mts.	BM 743		265+40	202+26	24/24	10
FRENCH GUIANA						
St. Laurent	CAS 14546	♀	270+x	211+x	28/28	10
TRINIDAD						
—	BM 746		270+36	204+25	22/22	6
—	BM 749		290+45	207+25	24/24	7

MATERIAL AND METHODS

The specimens used in this study are from the collections of the following institutions, to the authorities of which I am much indebted for the loan:

AMNH	American Museum of Natural History, New York City
BM	British Museum (Natural History), London[1]
CAS	California Academy of Sciences[1]
CM	Chicago Natural History Museum
DZ	Departamento de Zoologia (formerly of Museu Paulista), São Paulo, Brasil
IB	Instituto Butantan, São Paulo, Brasil
MCZ	Museum of Comparative Zoölogy at Harvard College, Cambridge, Mass.
SU	Stanford University Museum of Zoölogy, Palo Alto, California.
USNM	United States National Museum, Washington, D. C.

The localities involved were located chiefly by means of the maps published by the American Geographical Society. Government maps of the various countries and collectors' notes were also used.

The statistical analysis is founded on 9 basic samples. Three of these are homogeneous: that from Iquitos, composed of 18 specimens; that from Manaus, of 10; and that from Paramaribo, of 6. The variability of these three samples furnished a check on the adequacy of the remaining six. The latter are composed of specimens from restricted areas of uniform physiographic and climatic features. These samples include: Panama, 10 specimens from the Canal Zone and neighborhood; "Colombian Andes", 8 specimens from Medellin, Muzo, Payme and Honda; "Ecuadorian Andes", 6 specimens from Riobamba plus 1 from "between Baños and Canelos"; "Northern British Guiana", 6 specimens from Georgetown, Kamakusi, Kalacoon and Kaieteur; Trinidad, 16 specimens from various parts of the island; Ucayali River, 10 specimens from localities on the Ucayali between Reforma and Pucallpa.

Between several of these localities specimens of intermediate places are available.

Between Manaus and the "Colombian Andes" one small sample from Cucuí (3 specimens) and another from Villavicencio (4 specimens) provide opportunity for the study of intergradation. Other localities in Colombia are not included in the sample denominated "Colombian Andes": Barranca Bermeja, on the Magdalena, not included because of its situation in a valley, while the remaining localities are in the uplands; Rio Frio, in the Santa Marta region, and Riocito, in Venezuela, for the obvious reason of distance (see Map 1); and 3 localities,

---

[1] The material belonging to these institutions arrived too late for statistical treatment. They brought, however, no modifications to the results already obtained. The localities are included in Map 1 and nowhere else.

2 in the Chocó (Andagoya and Las Animas Creek, tributary to the Quito River, on the upper Atrato) and 1 in the adjacent Valle del Cauca (San Pedro) which are of interest because they are situated west of the Cordillera Occidental; these 3 localities are here called the sample from the Chocó.

Between Manaus and Iquitos we have a small sample (3 specimens) from Leticia. Between Iquitos and the Ecuadorian Andes there is a very interesting series: Cenipa River, Pastaza River, mouth of Santiago River, Avila and Luoula, on the Upano River. On the Pacific slope of the Ecuadorian Andes we have Bucay and the Daule River.

From between Manaus and British Guiana material from 2 localities is available: Vista Alegre on the Branco River and the Marudi River, tributary of the Kuyuwini River.

From Dutch Guiana 3 specimens labelled simply "Surinam" must probably come from the interior and may be considered, with due reserve, as intermediate between Paramaribo and Manaus.

Some Brasilian specimens present a problem. No suitable sample could be assembled from the sparse material. One specimen labelled only "Pará" is not useful because Pará is a very large state and, from the point of view of the geographical relationships here examined, a complex one. This is not the case with a specimen from the State of Maranhão that may be considered between the Amazon Valley and the State of Ceará. Finally, 3 most surprising specimens from "Santa Maria", collected by Maximilian, Prince of Wied Neuwied, were a problem until Dr. Oliverio Pinto (of the Dep. de Zoologia, São Paulo) definitely ascertained the precise locality to be an old Jesuit fazenda on the lower Ilheus River.

As to the statistical methods used, they were the simplest possible. They can be found in Simpson and Roe (1939), to whose work reference is made at suitable places, saving thus the necessity of explaining them at length. Klauber's methods were applied according to his papers, duly quoted in their appropriate context. In some cases Fisher (1948) was used; reference is made to chapter and section, instead of page, to make easier the use of older editions.

All the statistical tests were performed with the aid of Fisher and Yates' (1949) tables. In the calculations use was made of Barlow's (edited by Comrie, 1944) and Miner's (1947) tables.

No significant sexual differences were found in the samples analyzed. Consequently all the samples were treated without reference to sex. The small size of the samples and the preliminary character of this study warrant this procedure.

Finally, no attempt was made at uniformity of statistical treatment. The methods employed were those found best suited for the individual problems under investigation.

GEOGRAPHICAL DIFFERENTIATION OF SINGLE CHARACTERS.

1. Number of body annuli.

The number of body annuli is one of the best taxonomic characters of the amphisbaenians. Consistent counts, however, are not easy to obtain, as the annuli are not always regular and there are many partial doublings and splittings.

A method of counting was devised that afforded fairly consistent results with a minimum of time and effort. The specimen is held under the microscope by the operator's left hand; the tail, turned forward, is held between the middle and index fingers of the same hand while the thumb presses the abdomen. The annuli are counted along a line to the left of the medio-ventral line (to the right of the operator). A first count is made craniad and a second one caudad along the same line. The foremost annulus to be counted is the first complete one back of the oral commissure and the hindmost the one that bears the preanal pores. The two counts usually agree and the result is then recorded. If they do not agree, as is the case with specimens badly twisted or desiccated, 5 counts (3 in one and 2 in the opposite direction) are then made and the rounded mean recorded.

TABLE 2

Amphisbaena fuliginosa

Number of body annuli of 9 basic samples

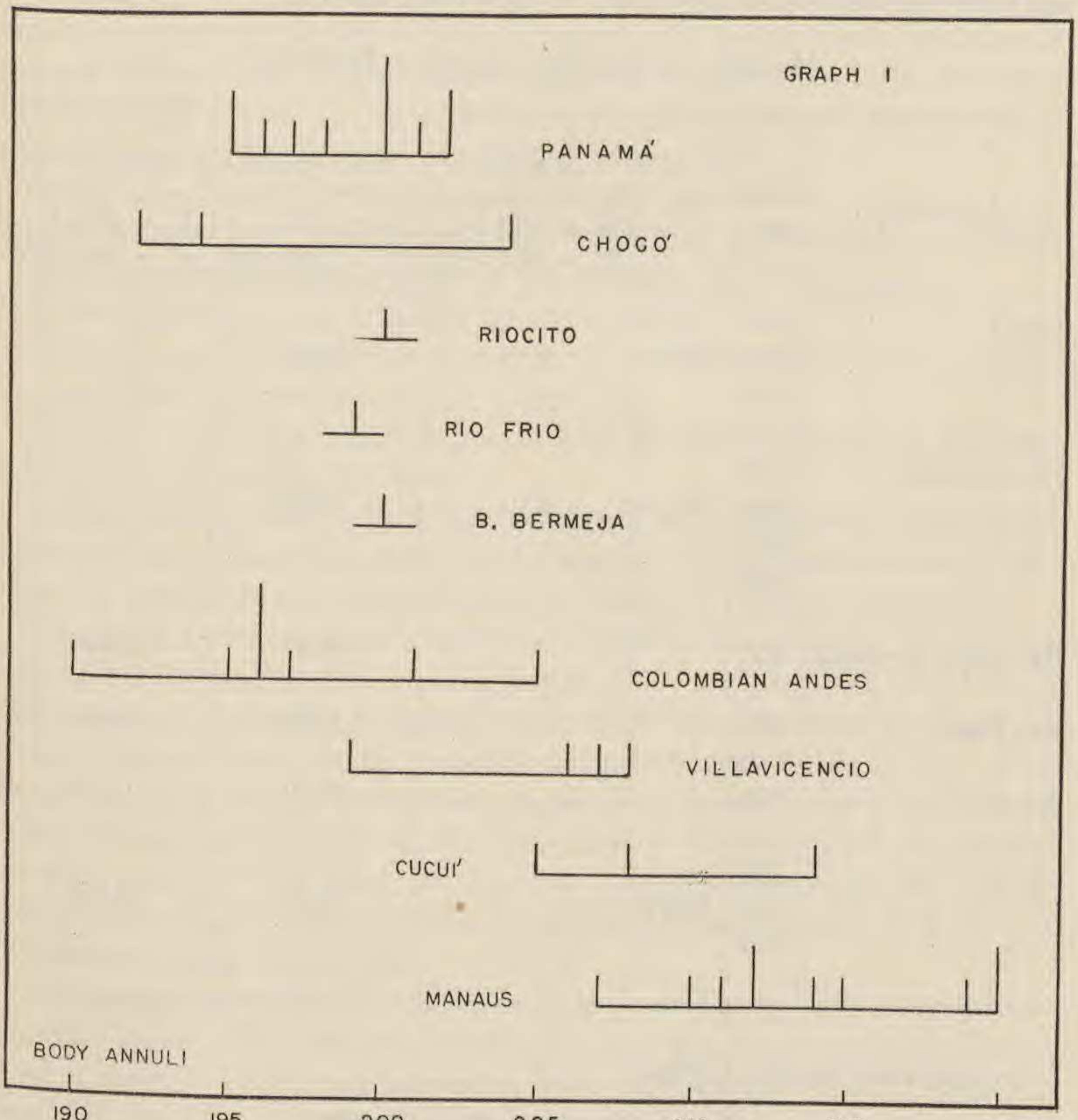
Localities	*N*	*R*	*M*	σ	*V*
Manaus	10	207–220	214.0 ± 1.41	4.5 ± 1.00	2.1 ± 0.5
Colombian Andes	8	190–205	197.0 ± 1.56	4.4 ± 1.10	2.2 ± 0.6
Panama	10	195–202	198.4 ± 0.81	2.6 ± 0.57	1.3 ± 0.3
Iquitos	18	204–213	207.7 ± 0.62	2.6 ± 0.44	1.3 ± 0.2
Ucayali River	10	204–215	210.3 ± 1.05	3.3 ± 0.75	1.6 ± 0.4
Ecuadorian Andes	7	197–205	202.1 ± 1.16	3.1 ± 0.82	1.5 ± 0.4
N. British Guiana	6	199–213	206.0 ± 2.08	4.7 ± 1.47	2.3 ± 0.7
Paramaribo	6	196–207	203.2 ± 1.85	4.5 ± 1.31	2.2 ± 0.6
Trinidad	16	202–212	206.3 ± 0.72	2.9 ± 0.51	1.4 ± 0.2

The statistics calculated for the 9 samples above mentioned are presented in Table 2. In this and similar tables

N	is the number of individuals in the sample
R	is the observed range of the variable
M	is the arithmetic mean
σ	is the standard-deviation
V	is the coefficient of variation.

The figures that follow these statistics, separated by a ± signal, are the respective standard-errors (Simpson & Roe, 1939: 85, 107, 112, 121, 149).

Inspection of this table shows that homogeneity of the several samples is not to be expected. Analysis of variance shows them to be heterogeneous (Fisher, 1948: 7, 40, 41).



Graph 1. *A. fuliginosa.* Variation of the number of body annuli in the territory between Manaus and Panama.

The sample with the highest mean is seen to be Manaus (214.0); the lowest means are to be found in the Colombian Andes (197.0) and Panama (198.4).

Analysis of variance among these three samples shows that they cannot have been drawn from the same population. Differences between the Colombian and Panamanian samples are not significant, even if the coefficient of variation is low in the sample from Panama. Both the Colombian and Panamanian samples differ significantly from the Manaus one.

TABLE 3

Amphisbaena fuliginosa — Number of body annuli. Probabilities of the *t* test between the basic samples and intergrading material.

Manaus — Colombian Andes — Panama

Localities	*Body ann.*	*M*	*Manaus*	*Col. Andes*	*Panama*
			M = 214.0 *R = 207–220*	*M = 197.0* *R = 190–205*	*M = 198.4* *R = 195–207*
Cucuí	205 208 214	209.0	0.10	0.01	
Villavicencio	199 206 207 208	205.0	0.01	0.001	
Barranca Bermeja	200			0.50	0.55
Rio Frio	199			0.65	0.80
Riocito	200			0.50	0.55
Chocó	192 194 201	195.7		0.70	0.20

In this and similar tables

M	is the mean of the samples
R	their observed ranges

The variation in the number of body annuli along this line is shown in Graph 1, wherein it may be noted that Cucuí and Villavicencio are represented by intermediate specimens. The intermediate character of these samples may receive numerical expression. Taking the difference between the mean of the larger samples (basic) and the mean of the small intermediate samples (or single specimens) we can calculate the respective value of *t* (Simpson & Roe, 1939: 209–210). This *t* corresponds to a probability of such a difference (or a larger one) arising by chance between samples taken at random from the same population. This probability is a good enough estimate of the closeness of the intergrades to the contrasted samples. Table 3 presents these probabilities (approximate values) for the line here discussed (Manaus-Colombian Andes-Panama).

The figures in the table are the probabilities that differences such as the ones observed occur within homogeneous populations because of sample fluctuations. Probabilities equal or smaller than 0.05 (5%) are taken as significant, i.e., indicate that the probability of the two samples belonging to the same population is negligible.

From the data in Table 3 it may be concluded that:

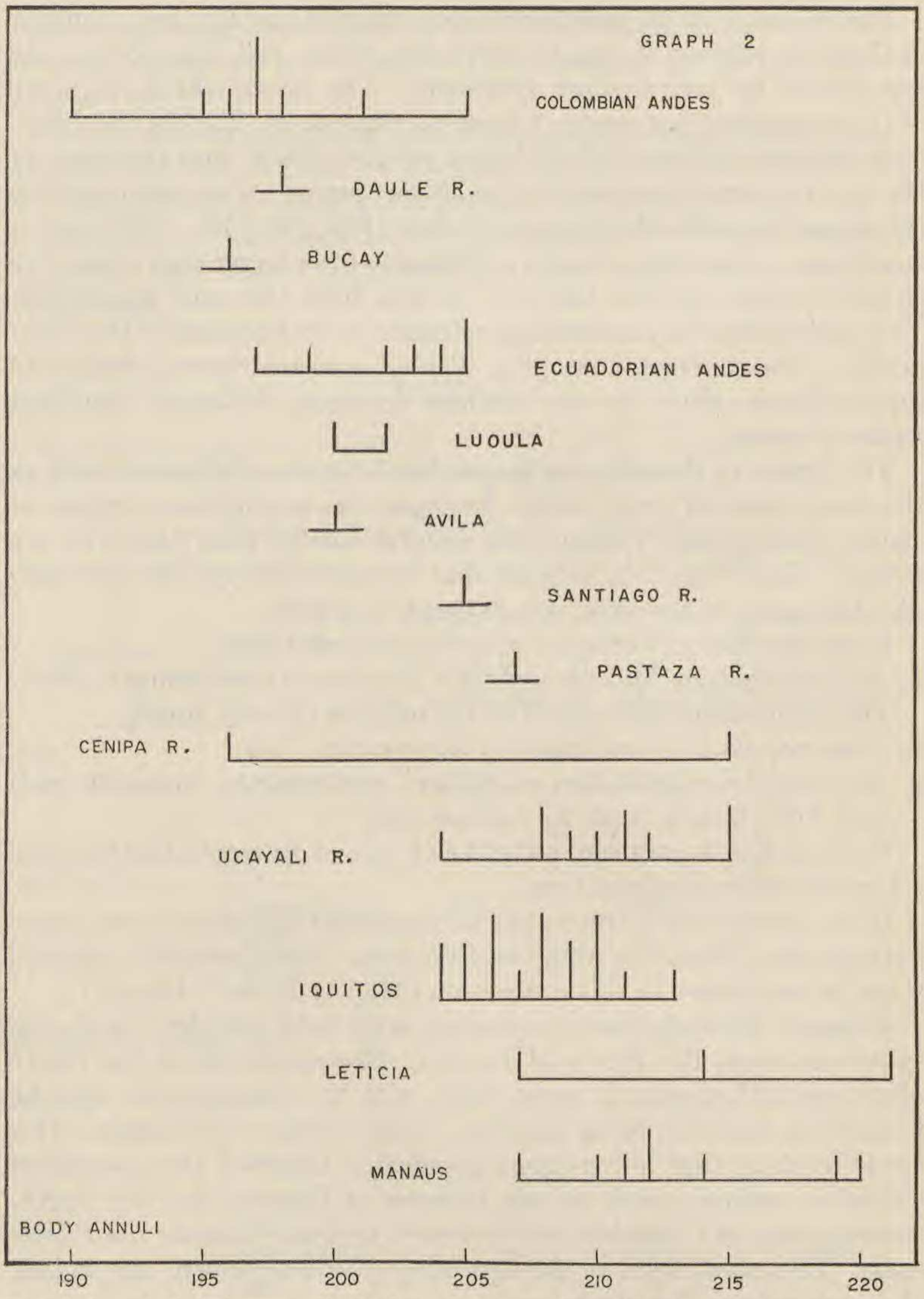
a. the samples from Manaus and the Colombian Andes belong to different populations with regard to the number of body annuli;
b. these populations are linked by intergrades;
c. the zone of intergradation comprises Cucuí (near its Amazonic end) and Villavicencio (near its Andean end).

We have here what seems to be the picture of differentiation between a lowland and a highland form.

It has already been noted that no significant differences were found between the Colombian Andes and Panama. Other available material must be considered in this connection (Map 1, Table 3, Graph 1).

Barranca Bermeja shows agreement with both samples. So do the specimens from Rio Frio and Riocito. The sample from the Chocó offers special interest: it agrees both with the Panamanian and the Colombian material, being possibly a shade nearer to the latter. This tends to show that a low-count population found in the uplands of Colombia extends north to the Isthmus of Panama and the northwestern coast of Colombia; to the west it probably reaches the Pacific coast. The exact limits to the east cannot be ascertained, due to lack of material from Venezuela.

Let us now consider the variation of the number of body annuli from another angle. The sample from Riobamba and neighborhood (Ecuadorian Andes) differs significantly from the Manaus one. Using the same methods as for the Colombian sample we may investigate the existence of intergradation in the case of these samples (Graph 2, Table 4).



Graph 2. *A. fuliginosa.* Variation of the number of body annuli in the territory between Manaus and the Pacific coast of Ecuador. Colombian sample introduced for comparison.

Specimens from Leticia agree entirely with those from Manaus. Iquitos material, however, is definitely intermediate and intergradation proceeds from Iquitos up to the foothills of the Andes (Avila, Luoula) where agreement is reached with the upland material. In this connection it is interesting to note that counts of the two specimens from Rio Cenipa approach both limits of the distribution (196 and 219).

Two amphisbaenids from near the Pacific coast (Daule R. and Bucay) agree with the upland series, although both provide values closer to the lower limit of the range; they agree much better with the Colombian material.

The sample from the Ucayali River presents a mean significantly different from both Manaus and Iquitos, and closer to the latter.

TABLE 4

Amphisbaena fuliginosa — Number of body annuli. Probabilities of the t test between the basic samples and intergrading material.

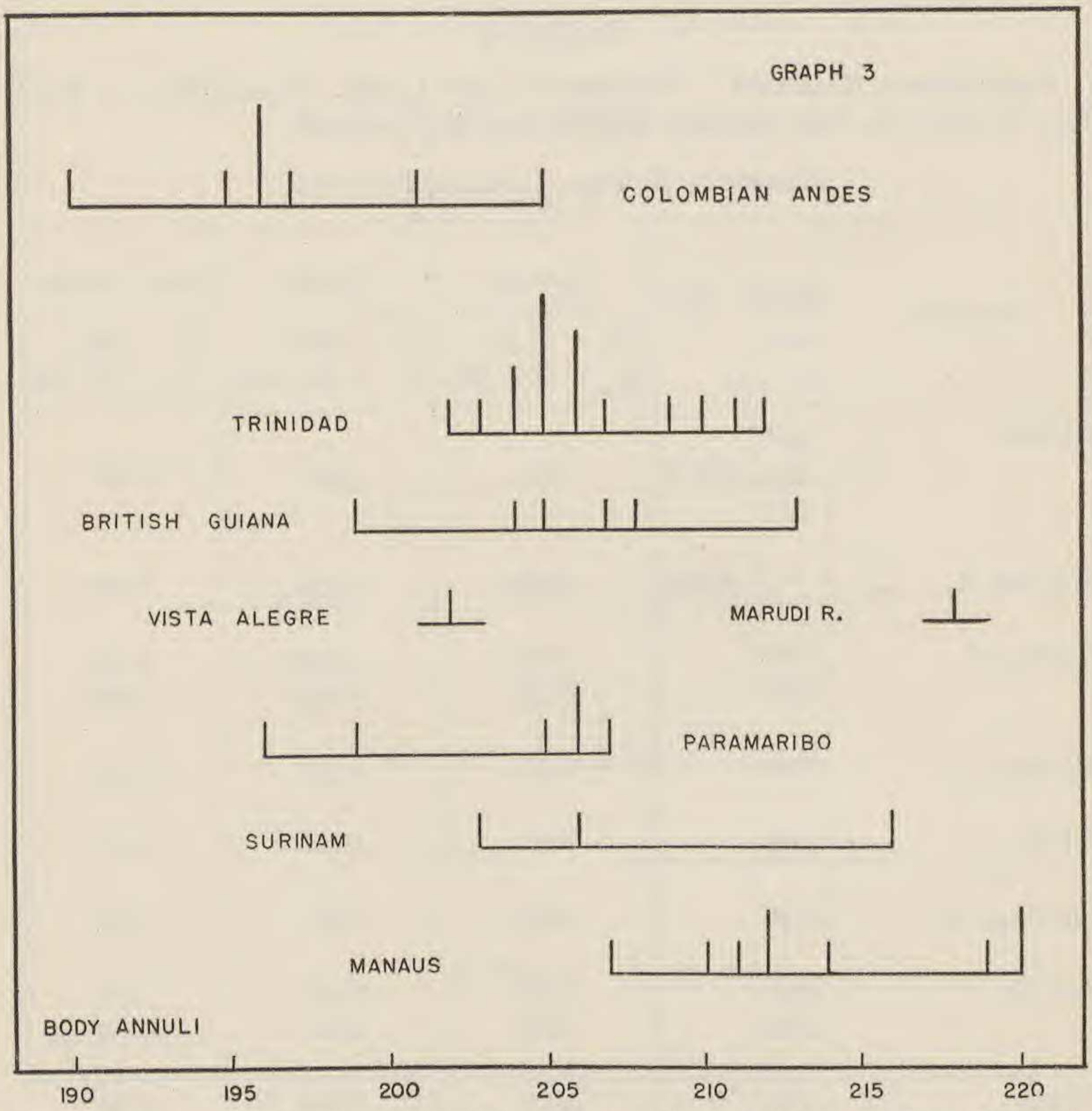
Manaus — Iquitos — Ecuadorian Andes

Localities	*Body ann.*	*M*	*Manaus*	*Iquitos*	*Ecuad. Andes*
			$M = 214.0$ $R = 207\text{–}220$	$M = 207.7$ $R = 204\text{–}213$	$M = 202.1$ $R = 197\text{–}205$
Leticia	207				
	214	214.0	1.0	0.01	0.001
	221				
Ucayali R.		210.3	0.045	0.035	0.001
Cenipa R.	196		0.001	0.001	0.10
	219		0.30	0.001	0.001
Pastaza R.	207		0.15	0.80	0.15
Avila	200		0.01	0.02	0.55
Santiago R.	205		0.075	0.30	0.40
Luoula	200		0.01	0.02	0.55
	202		0.03	0.04	0.99
Bucay	198		0.01	0.001	0.25
Daule R.	196		0.001	0.001	0.10

Comparing the Ecuadorian and Colombian material we see that they do not agree, but that the former is intermediate between the latter and the high count populations (as represented by Iquitos).

We can summarize variation in this region by stating that there are two distinct lowland populations (Manaus and Ucayali River) with high averages; these seem to intergrade between themselves and with a low count highland population. The intergradation belt comprehends the upper Amazon, the foothills of the Andes in Ecuador and Colombia and the Ecuadorian Andes.

The northern coast of South America is here represented by material from Trinidad[1], northern British Guiana and Paramaribo. (Graph 3, Table 5).



Graph 3. *A. fuliginosa.* Variation of the number of body annuli in the territory between Manaus and the northern coast of South America. Colombian sample introduced for comparison.

---

[1] Trinidad is taken here as representing the mainland stock that colonized the island. Even if there has been differentiation of the insular population, it will resemble the parent form rather than any other. This fact will receive fuller discussion in a later section.

These samples are shown by analysis of variance to be reasonably homogeneous, although Paramaribo shows a tendency toward low counts. The three samples differ significantly from Manaus both individually and taken together.

We have already commented upon the scarcity of intergrades in this region. The two specimens from Vista Alegre and from the Marudi River possess the same features as those from the Cenipa River; although the localities are very close, the values are far apart. The specimens from Surinam behave as colorless intergrades. These samples from the northern coast of South America also differ significantly from those of Colombia and Panama. They show values close to the ones found in Villavicencio and Iquitos, but significantly higher than the samples from Ecuador.

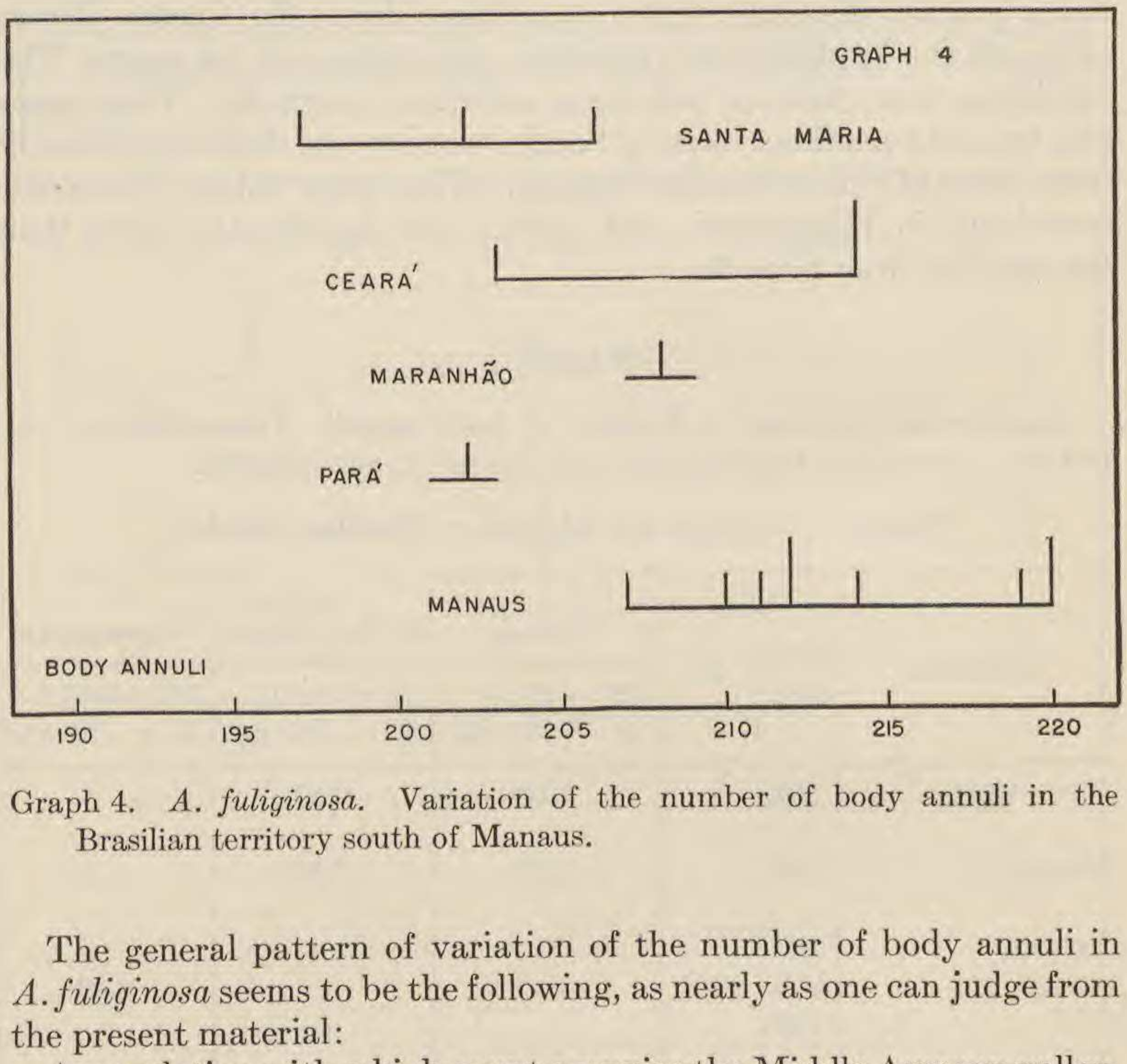
TABLE 5

Amphisbaena fuliginosa — Number of body annuli. Probabilities of the test of *t* between the basic samples and the intergrade material.

Manaus — Guianas and Manaus — Brasilian samples.

Localities	*Body ann.*	*M*	*Manaus*	*N. Brit. Guiana*	*Paramaribo*
			M = 214.0 *R = 207–220*	*M = 206.0* *R = 199–213*	*M = 203.2* *R = 196–207*
Vista Alegre	202		0.02	0.40	
Marudi R.	218		0.40	0.03	
Surinam	203				
	205	208.0	0.10		0.30
	216				
Pará	202		0.02		0.50
Maranhão	208		0.20		
Ceará	203				
	214	210.3	0.30		
	214				
Santa Maria	197		0.01		
	202	202.7			
	206				

The remaining Brasilian material includes samples with a peculiar distribution of values. The Maranhão and Ceará specimens, although not significantly different from the Manaus ones, provide lower values. The specimens from Santa Maria, however, differ significantly from those of Manaus, approaching the values found in those of Ecuador.

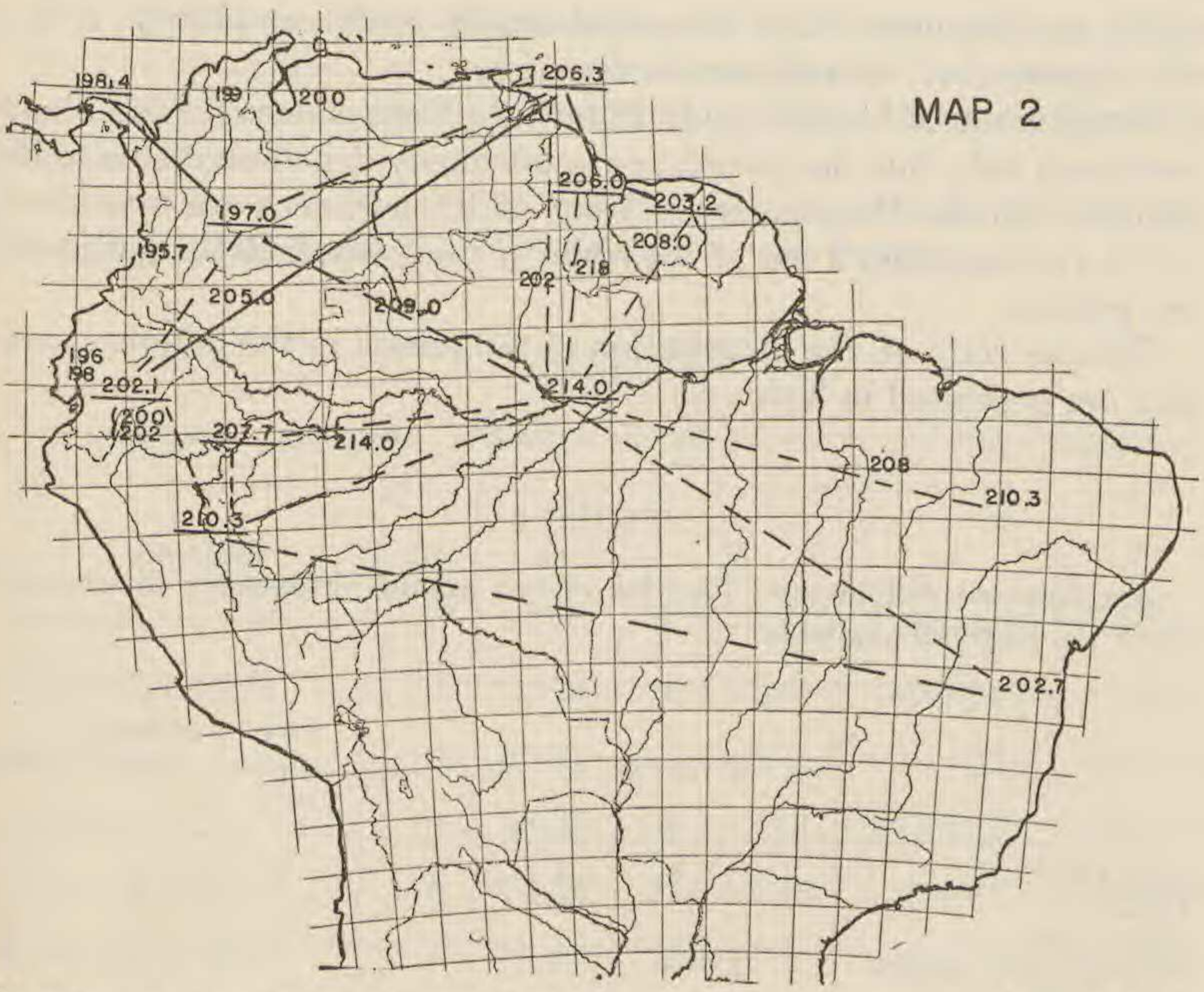


Graph 4. *A. fuliginosa.* Variation of the number of body annuli in the Brasilian territory south of Manaus.

The general pattern of variation of the number of body annuli in *A. fuliginosa* seems to be the following, as nearly as one can judge from the present material:

A population with a high count occupies the Middle Amazon valley, at least from Manaus to Leticia. Surrounding this population there is an interrupted ring of populations having low counts. Among those the lowest values are found in Colombia and Panama. Wherever critical material is available, intergradation between populations with high and low counts is evident.

These relationships are depicted in Map 2 and will be discussed later, together with the results of the study of variation of other characters.



MAP 2

Map 2. *A. fuliginosa.* Geographic differentiation of the number of body annuli. The decimal numbers are averages of samples; the underlined ones belong to the 9 major samples, the remainder to the small samples of 3 and 4 specimens. Integers refer to isolated specimens. The figures are placed on the approximate location of the place. The series between Iquitos and the Ecuadorian Andes has been partially suppressed to avoid overcrowding (see Graph 2). Broken lines between two numbers mean that the difference between them is statistically significant; solid lines that the difference is not significant.

2. Number of tail annuli

The number of complete tail annuli between and including the first one behind the cloaca and the tip of the tail is also a useful taxonomic character for the separation of species in the *Amphisbaenidae.* In some of them, however, there is an anatomical feature that deprives the character of much of its usefulness. In such forms as *A. mertensii* (Vanzolini, 1948), *A. fuliginosa, A. subocularis, A. spurrelii, A. slevini* and others the proximal annuli are of normal shape, resulting in a cylindrical segment of tail; there is, at the end of this segment, a shorter and a little narrower annulus, the ones distal to it being somewhat swollen. This shorter annulus is the commonest level for fractures, which are frequent. The truncated stump heals completely, a fact that has resulted in erroneous assumptions.

In the material for this study 28 out of 129 specimens (21.7%) have mutilated tails, but the percentage is unequally distributed among the samples. In the Panama series 5 out of 10 specimens are mutilated; in the Iquitos series 2 out of 18; while in the Ucayali River sample all are perfect.

The raw data on the distribution of tail annuli in the different samples are presented in Table 6.

TABLE 6

Amphisbaena fuliginosa — Number of tail annuli. Frequency distribution in all the material available.

Locality	*23*	*24*	*25*	*26*	*27*	*28*	*29*	*30*	*Total unbroken tails*	*Mutilated tails*	*Total*
MANAUS		2	3	3	1				9	1	10
Cucuí							1		1	2	3
Villavicencio			2	1					3	1	4
COLOMBIAN ANDES	1	3	2	1					7	1	8
Barranca Bermeja					1				1	–	1
Rio Frio			1						1	–	1
Riocito				1					1	–	1
Chocó		2	1						3	–	3
PANAMA	1	3			1				5	5	10
Leticia			1	1					2	1	3
IQUITOS				2	2	2	7	3	16	2	18
UCAYALI RIVER				2	1	3	4		10	–	10
Cenipa River									–	2	2
Pastaza River									–	1	1
Avila				1					1	–	1
Santiago River							1		1	–	1
Luoula					1				1	1	2
ECUADORIAN ANDES	1		1	2			1		5	2	7
Bucay			1						1	–	1
Daule River					1				1	–	1
Vista Alegre			1						1	–	1
Marudi River							1		1	–	1
N. BRITISH GUIANA		2	2	1					5	1	6
Surinam			1		1				2	1	3
PARAMARIBO			2	1	1				4	2	6
TRINIDAD		3	4	4	3				14	2	16
Pará									–	1	1
Maranhão									–	1	1
Ceará		1	1	1					3	–	3
Santa Maria						1	1		2	1	3
Total									101	28	129

The restricted range of variation of this variable does not favor study of intergradation by the methods used for the body annuli. The best results are achieved by using tests of significance of differences between means.

Inspection of Tables 6 and 7 shows that two samples present outstanding values among all: Ucayali River and Iquitos.

TABLE 7

Amphisbaena fuliginosa — Number of tail annuli in the basic samples.

Locality	*N*	*R*	*M*	*σ*	*V*
Manaus	9	24–27	25.3 ± 0.51	1.54 ± 0.36	6.1 ± 1.5
Colombian Andes	7	23–26	24.4 ± 0.38	1.00 ± 0.27	4.1 ± 1.1
Panama	5	23–27	24.4 ± 0.67	1.50 ± 0.44	6.2 ± 2.0
Iquitos	16	26–30	28.4 ± 0.32	1.27 ± 0.22	4.5 ± 0.6
Ucayali River	10	26–29	27.9 ± 0.38	1.20 ± 0.27	4.3 ± 0.9
Ecuadorian Andes	5	23–29	25.8 ± 0.97	2.18 ± 0.70	8.5 ± 2.7
N. British Guiana	5	24–26	24.8 ± 0.39	0.87 ± 0.27	3.6 ± 1.1
Paramaribo	4	25–27	25.8 ± 0.45	0.91 ± 0.32	3.6 ± 1.3
Trinidad	14	24–27	25.5 ± 0.29	1.07 ± 0.20	4.2 ± 0.8

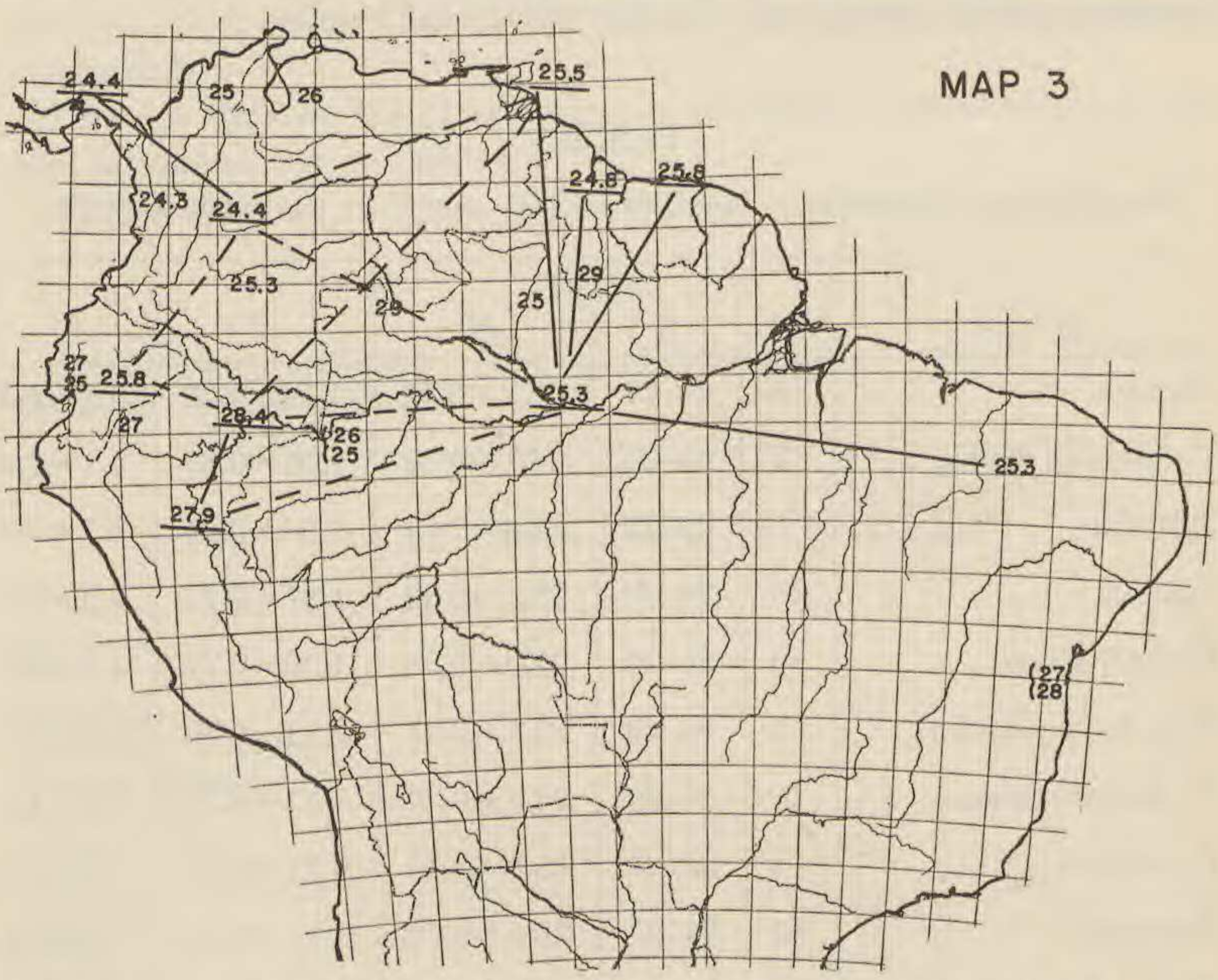
Both the samples from Manaus and from the Ecuadorian Andes differ significantly from the Iquitos and Ucayali samples. Among the remaining samples only one difference is found: that between the series from Colombia and the one from Trinidad. The difference between the Manaus and the Colombian Andes samples approaches the 0.05 level, but does not quite reach it.

The general picture of differentiation of the number of caudal annuli seems to be the following:

A population with high counts occupies the Ucayali River valley up to Iquitos. On the rest of the range there is some variation that does not seem to follow any definite pattern nor to be (with the present material) very extensive. The only break of continuity lies between Colombia and Trinidad. In this island and in the Guianas the values of this variate tend to be higher without reaching the ones found in Peru.

CORRELATION BETWEEN NUMBER OF BODY AND TAIL ANNULI

No significant correlations were found between the number of body and of tail annuli, either inside the various samples or (rank correlation) among all of them (Simpson & Roe, 1939).



Map 3. *A. fuliginosa.* Geographic variation of the number of tail annuli See caption under Map 2.

3. Number of segments to a midbody annulus

The number of segments that compose an annulus is usually given as the number of segments between the two lateral sulci, counted above and below these. They constitute useful taxonomic characters, but their determination and analysis are not simple.

A first point to be noticed is the definition of "midbody annulus". This expression has been used rather loosely. Schmidt (1936), feeling the need of a more rigorous definition, used the 100th annulus as the one on which to count the segments. This is decidedly an improvement on the old nomenclature, but it seems to me that such a strict definition of the annulus to be counted is not entirely desirable, due to the fact that there are no regular longitudinal or quincuncial rows of segments in *A. fuliginosa* or any other *Amphisbaena*. The number of segments per annulus is fairly constant for a given section of the trunk, but many irregularities (fusions, splittings or simple discordance of margins of segments) are frequent. It seems to me that the best practice is to count the segments on the hundredth and some adjacent annuli. In a great many cases they will agree. In an appreciable number of instances, however, this will not happen; in such a case the mode of the counts will be taken as the value sought.

It will be seen that all values recorded here are even. The explanation is simple. The variate in question is not really the "number of segments to a midbody annulus", but the "number of segments to a midbody half-annulus". As the amphisbaenians are limbless lizards, we are inclined to forget the bilateral symmetry and treat both sides together as a single unit. This problem has been analyzed by Klauber (1941) for dorsal rows of scales of snakes and I doubt if I could add anything to Klauber's comments.

One of the most useful statistics commonly employed in systematics is the observed range. Non-overlapping of ranges of one or more variables is one of the better criteria for separation of related forms. There is no inconvenience in such a use of the total number of segments as a "key" character. For statistical treatment, however, it is necessary to reduce the data to half-bodies. This is done by assigning to each half-body a frequency of one-half unit. A specimen with both sides equal (as is the case with all in this connection, but not all in the forthcoming case of preanal pores) will contribute one unit to the respective class. Consideration of each half-body as a full unit would unduly increase the number of degrees of freedom.

The data pertaining to dorsal and ventral segments are presented in Tables 8 and 9. Table 9 will do instead of graphs to show the nature of intergradation, for which this character is of little value.

Inspection of these tables and tests of significance of differences between means suggest that the samples from northern British Guiana, Trinidad, Colombian Andes, Panama, Ecuadorian Andes and Iquitos agree very well among themselves. The Ucayali River sample agrees with the Ecuadorian and Iquitos ones in dorsals, but differs in ventrals. All the isolated localities within this territory fit well into the general picture. Manaus differs from Iquitos, Ucayali River, and Colombian Andes. Leticia might be transitional in dorsals but is decidedly Amazonic in ventrals. The two specimens from Vista Alegre and Marudi River may be called intermediate. Paramaribo agrees entirely with Manaus, differing from northern British Guiana in dorsals. One specimen from "Surinam" presents the highest count of dorsals (28); the other one available is a rather low 22.

TABLE 8

Amphisbaena fuliginosa — Number of segments on a mid-body annulus. Distribution of frequencies for all the available material.

	Dorsal					*Ventral*						
Locality	*20*	*22*	*24*	*26*	*28*	*18*	*20*	*22*	*24*	*26*	*28*	*Total*
MANAUS		2	6	2				2	7	1		10
Cucuí	1	2					1	2				3
Villavicencio			3	1					1	3		4
COLOMBIAN ANDES	2	4	2				3	2	3			8
Barranca Bermeja	1							1				1
Rio Frio		1					1					1
Riocito			1							1		1
Chocó		2	1				1		2			3
PANAMA		5	5					6	4			10
Leticia	1		1		1			1	2			3
IQUITOS	2	15	1				1	16	1			18
UCAYALI RIVER	4	6				2	2	6				10
Cenipa River	1	1						2				2
Avila	1							1				1
Santiago River	1							1				1
Luoula	1	1						2				2
ECUADORIAN ANDES	1	6						6	1			7
Bucay		1						1				1
Daule River			1				1					1
Vista Alegre		1							1			1
Marudi River			1					1				1
N. BRITISH GUIANA	1	4	1				1	2	3			6
Surinam		1			1				1	1		2
PARAMARIBO			3	3			3	2	1			6
TRINIDAD	6	7	2			2	6	6	1			15
Pará				1							1	1
Maranhão			1					1				1
Ceará	1	1	1				1		2			3
Santa Maria				3					1	2		3
												127

As for Brasilian specimens, the Santa Maria series agrees with that from Manaus rather than with the samples having low counts. The specimen from Pará has the maximum count, 28. The series from Ceará seems to tend toward low values.

These relationships, as seen in Map 4, seem to follow a pattern in which specimens from the western part of the range present lower counts than those from the eastern.

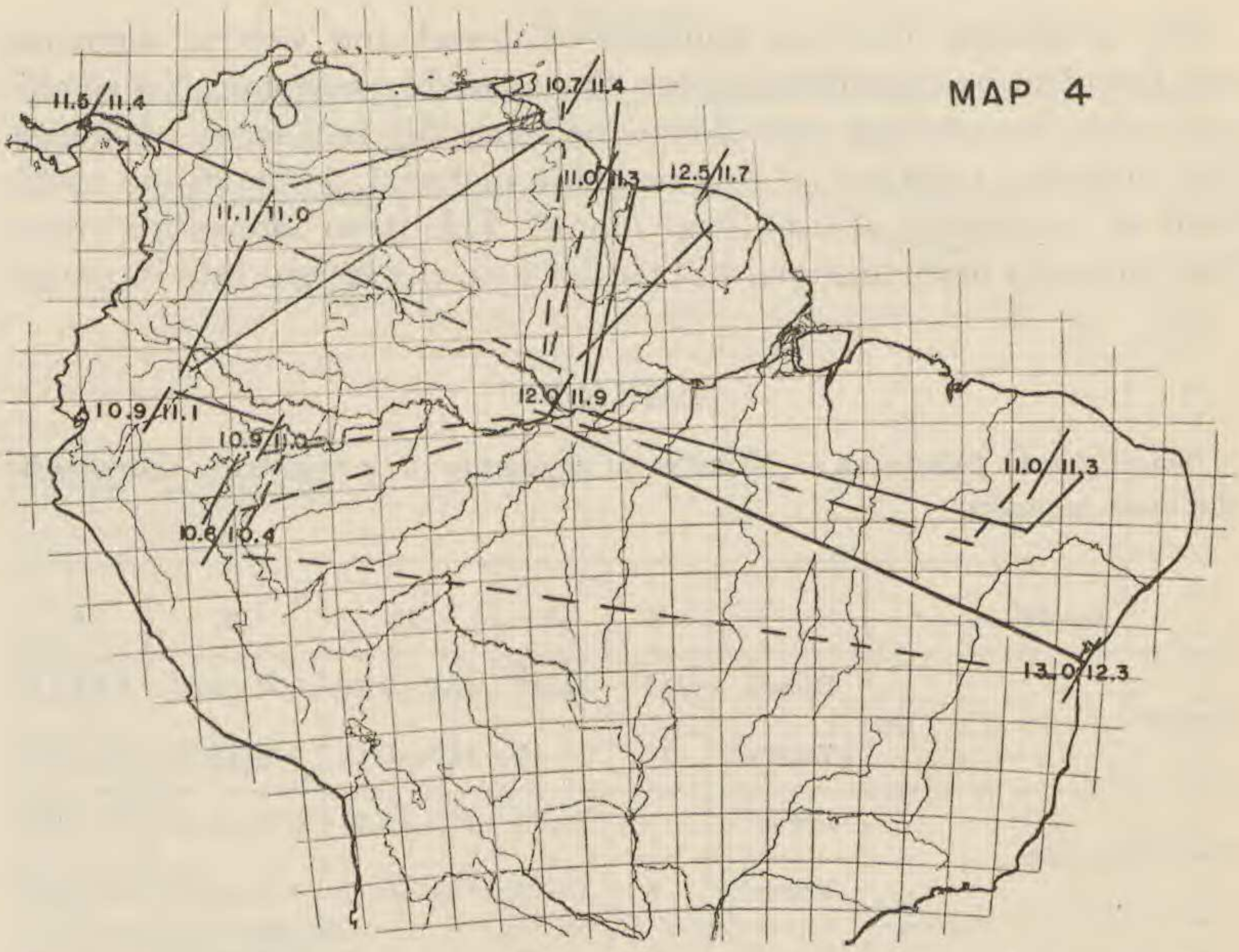
It is interesting to note that in 6 out of 9 samples the means for dorsal and ventral segments differ by 0.2 or less; in 1 sample by 0.3 and in 2 (Panama and Trinidad) by 0.8 and 0.7, respectively.

No correlation between numbers of dorsal and ventral segments was found to be significant within the available samples. No significant rank correlations were found between the two series of means. But, lumping together all the available material, a significant coefficient of correlation of 0.440 was found. This is an interesting situation, but only more material will permit a deeper insight into its cause.

TABLE 9

Amphisbaena fuliginosa — Number of segments on a mid-body annulus in the basic samples.

Locality		*N*	*R*	*M*	*σ*	*V*
Manaus	Dorsal	10	11–13	12.0±0.21	0.67±0.15	5.6±1.3
	Ventral	10	11–13	11.9±0.18	0.57±0.13	4.8±1.1
Colombian Andes	Dorsal	8	10–13	11.1±0.37	0.99±0.26	8.9±2.2
	Ventral	8	10–12	11.0±0.33	0.95±0.23	8.6±2.2
Panama	Dorsal	10	11–12	11.5±0.17	0.53±0.12	4.6±1.0
	Ventral	10	11–12	11.4±0.16	0.52±0.12	4.6±1.1
Iquitos	Dorsal	18	10–12	10.9±0.10	0.42±0.07	3.9±0.6
	Ventral	18	10–12	11.0±0.08	0.34±0.06	3.1±0.5
Ucayali River	Dorsal	10	10–11	10.6±0.16	0.52±0.12	4.9±1.1
	Ventral	10	9–11	10.4±0.27	0.84±0.19	8.1±1.8
Ecuadorian Andes	Dorsal	7	10–11	10.9±0.16	0.38±0.12	3.5±0.8
	Ventral	7	11–12	11.1±0.16	0.38±0.12	3.4±0.8
N. British Guiana	Dorsal	6	10–12	11.0±0.26	0.63±0.18	5.7±1.7
	Ventral	6	10–12	11.3±0.24	0.82±0.24	7.3±2.1
Paramaribo	Dorsal	6	12–13	12.5±0.22	0.55±0.16	4.4±1.3
	Ventral	6	11–13	11.7±0.33	0.82±0.24	7.0±2.0
Trinidad	Dorsal	15	10–12	10.7±0.18	0.70±0.13	6.5±1.2
	Ventral	15	10–13	11.4±0.21	0.83±0.15	7.3±1.3



Map 4. *A. fuliginosa.* Geographic variation of the number of segments to a mid-body annulus. The 9 basic samples are shown, plus the ones from Sta. Maria and Ceará. The figures to the left of the mark / represent the mean number of dorsal segments; the figures to the right, the mean number of ventral segments. See also caption to Map 2.

4. Number of preanal pores

No evidence of sexual dimorphism was found in this character. This does not mean the results obtained were decisive evidence of sexual homogeneity in pore number. It only means that the present data, admittedly insufficient for such an analysis, do not indicate the presence of sexual dimorphism. As sexual differences were found in no other character, this reasoning must be extended to all the cases. The sex is not easy to ascertain in the larger species of *Amphisbaena,* and I expect my percentages of females to be a little higher than the true population values.

As in the case of segments to a midbody annulus, it is more exact to consider the preanal pores separately for the two sides. In this instance again the range is of taxonomic importance and no inconvenience is found in the use of the range and modal value as the only data provided in keys or differential diagnoses. The addition of other statistics would even be cumbersome and of little value.

The small number of classes and discrete variation would perhaps favor the use of qualitative statistical methods for this variate. The small number of individuals in the extreme classes, however, proves bothersome to such tests and it was thought better to follow the methods used before.

Table 10 shows an overall picture of the variation of this character. The respective means and standard-errors are presented in Table 11.

TABLE 10

Amphisbaena fuliginosa — Number of preanal pores. Distribution of frequencies in all the available material.

Locality	*Preanal pores*					*Total*
	6	*7*	*8*	*9*	*10*	
MANAUS			9	1		10
Cucuí	1		2			3
Villavicencio			3	1		4
COLOMBIAN ANDES	3	2	2			7
Barranca Bermeja			1			1
Rio Frio		1				1
Riocito			1			1
Chocó	2		1			3
PANAMA			6	4		10
Leticia			2		1	3
IQUITOS	1		17			18
UCAYALI RIVER		3	7			10
Cenipa River		1	1			2
Pastaza River			1			1
Avila			1			1
Santiago River			1			1
Luoula			1	1		2
ECUADORIAN ANDES		1	5	1		7
Bucay		1				1
Daule River			1			1
Vista Alegre			1			1
Marudi River			1			1
N. BRITISH GUIANA			4	2		6
Surinam			2	1		3
PARAMARIBO			4	1	1	6
TRINIDAD	6	2	8			16
Pará			1			1
Maranhão			1			1
Ceará			2		1	3
Santa Maria			1	1	1	3
Total						128

The samples from the Colombian Andes and Trinidad agree with each other, but differ significantly from all the remainder. No other significant differences were found, although the southwestern samples seem to tend toward lower values than the northern ones.

As to the scattered material, Cucuí and Villavicencio seem to be intermediate between Manaus and Colombia. All the rest of the material agrees with the samples from adjacent areas.

TABLE 11

Amphisbaena fuliginosa — Number of preanal pores. Means of the basic samples.

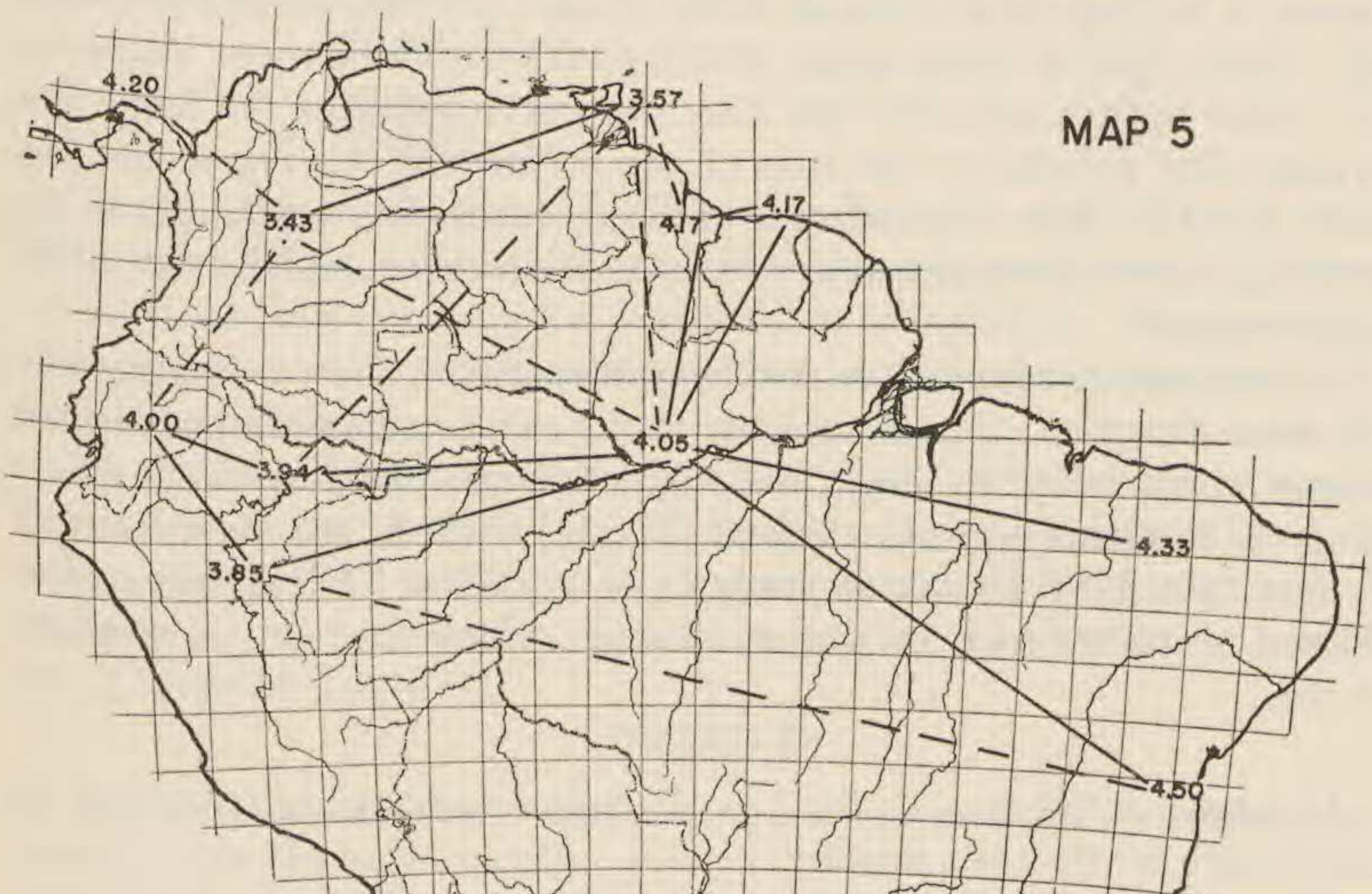
Locality	*N*	*M*
Manaus	10	4.05 ± 0.11
Colombian Andes	7	3.43 ± 0.20
Panama	10	4.20 ± 0.13
Iquitos	18	3.94 ± 0.55
Ucayali River	10	3.85 ± 0.11
Ecuadorian Andes	7	4.00 ± 0.15
N. British Guiana	6	4.17 ± 0.14
Paramaribo	6	4.17 ± 0.14
Trinidad	16	3.57 ± 0.13

The general picture with reference to preanal pore counts seems to be one of a widespread population with a range of 7–10 pores, but with a heavy concentration on 8. Within this population we find another one, presumably continuous, occupying Colombia and Venezuela to Trinidad.

5. Relative tail length

The study of body proportions has received in recent years a great impetus, chiefly since Huxley and Teissier's first studies on allometric curves. Unfortunately, most of the studies published using this and other methods lack a more precise statistical treatment, a fact that reduces their usefulness to a minimum. Klauber (1938, 1943) has published extremely important papers on the subject of body proportions in snakes and the methods of his 1943 paper are here applied without change to *Amphisbaena*, a limbless lizard.

The measurement of museum specimens of *Amphisbaena*, especially the bulkier species, is not very easy. The body is usually twisted and the bends are hard to straighten out. Best results were obtained by me with a flexible ruler. The body length is measured along the ventral midline, from snout to vent; the tail length also, preferably ventrally from vent to a plane that passes tangentially to the tail tip. The body lengths were recorded to the nearest 5 mm; the tail lengths to the nearest 1 mm (Simpson & Roe, 1939: 19–33). Perfect consistency is rarely obtained for body length; the data here presented are means of 3 measurements, differing usually by 5% to 10%. Tail length is not hard to measure, and consistency is usually easy to obtain. The specimens were shuffled and measured without reference to locality data, to avoid bias. In plotting the points, the less closely fitting ones were checked; no reason for change was seen in more than 90% of the cases; the few mistakes were made in copying.



Map 5. *A. fuliginosa*. Geographic variation of the number of preanal pores. Averages of the basic samples shown. See also caption to Map 2.

Several of the samples were too small for a reliable fit. When possible these were enlarged by adding the specimens from adjacent territories shown not to differ from them in other characters. Sample "Colombian Andes" was replaced by sample "Colombia", which included, besides the former, the specimens from Barranca Bermeja, Rio Frio, Riocito and the Chocó. Sample "Ecuadorian Andes" including the material from Bucay, Daule River and Luoula became sample "Ecuador". Sample "Paramaribo" including 3 specimens from Surinam became sample "Dutch Guiana". The remainder were not altered.

The regression of tail length on body length seems to obey a linear relationship in *A. fuliginosa*. In *A. alba* and *A. darwinii darwinii* (Vanzolini, in press) I found a curve with an upper plateau, closely resembling a Gompertz curve. This is most probably due to lack of correlation in adult age. During the period of growth the two variables appear to be correlated because both present a strong correlation with age. Since one of them stops growing, the curve changes character and when both reach ultimate size, the curve assumes the form of a straight line parallel to the axis of the x (form of the regression line when $r = 0$). The concordance of these successive stages gives the resulting curve the appearance of a saturation curve, which is theoretically baseless.

In the present case one or two samples seem to show a tendency in the same direction. Since exclusion of the suspected specimens did not change appreciably the slope, a straight line was fitted to all the specimens by the least squares method (Fisher, 1948; **5**, 26). Goodness of fit was tested by means of analysis of variance. Allometric curves showed no better and, in almost all cases, worse fits, and so were rejected.

TABLE 12

Amphisbaena fuliginosa — Data on the linear regression of tail length on body length for the basic samples.

Locality	*N*	*a*	*b*	*Sy.x*	*r*
Manaus	9	4.35	0.114	2.62	0.93
Colombia	13	2.24	0.142	2.20	0.97
Panama	5	0.76	0.145	0.50	0.996
Iquitos	15	0.62	0.170	4.06	0.88
Ucayali River	9	− 2.52	0.173	2.75	0.97
Ecuador	8	− 6.25	0.177	3.59	0.93
N. British Guiana	5	6.92	0.113	2.84	0.98
Dutch Guiana	6	2.98	0.138	2.30	0.990
Trinidad	13	−16.03	0.217	1.49	0.97

The data pertaining to the graduated lines are presented in Table 12. In this table

N	is the number of individuals in the samples;
a, b	are the terms of the linear equation $y' = a + bx$ in which x is the body length and y' the calculated tail length;
$s_{y.x}$	is the standard error of estimate and
r	is the coefficient of linear correlation (Simpson & Roe, 1939).

Perusal of this table shows that the samples may be separated into four groups, according to the slope (*b*):

1.	Northern British Guiana	b = 0.113
	Manaus	0.114
2.	Colombia	0.142
	Panama	0.145
	Dutch Guiana	0.138
3.	Iquitos	0.170
	Ucayali River	0.173
	Ecuador	0.177
4.	Trinidad	0.217

Testing the significance of differences between various pairs of coefficients (Fisher, 1948: 5, 27), we find the only consistent differences to be those between Trinidad and the first two groups. This would rob this grouping of its significance; further analysis, however, shows that this is unnecessary.

There is, as Klauber points out (1943: 40) no point in comparing the regression constants *a* for different samples. The real interest lies in the comparison of tail length at various moments of life, as expressed by suitable body lengths. To obtain the desired standard body lengths, let us inspect Table 13.

TABLE 13

Amphisbaena fuliginosa — Body- and tail length of smallest and largest specimens in the basic samples.

Locality	*Smallest*	*Largest*
Manaus	152+x	330+40*
	170+21	
Colombia	115+19	405+58**
Panama	240+36	350+52
Iquitos	245+39	450+75
Ucayali River	105+16	365+62
Ecuador	200+x	380+64
	220+34	
N. British Guiana	195+29	420+55
Dutch Guiana	135+21	370+x
		350+51
Trinidad	195+25	310+x
		280±42
*Cucuí		390+x
Leticia		340+x
**Villavicencio		440+x

Looking for the length at birth, we see that the smallest specimens recorded measure 105 mm and 115 mm. There is one specimen from Paramaribo measuring 90 mm, but this has not been included because it has an abnormally low number of body annuli, being, in all probability, a non-viable juvenile. So the length of 110 mm was taken as representing the first stage in the life history of *A. fuliginosa*. Several samples do not include any specimen even approaching this size, but I think it is relatively safe to assume that the extent of variability at birth will not be so large as to invalidate these comparisons.

For the adult size, we find the longest specimen to be one measuring 450 mm from snout to vent. Three samples have specimens exceeding 400 mm: Iquitos, British Guiana and Colombia. The remainder, however, excepting that from Trinidad, present values above 350 mm. So body lengths of 350 mm and 400 mm were chosen to test differences in full grown adults.

In an effort to compare individuals still growing but already presumably in reproductive age, one further standard length, 250 mm, was introduced.

Tail lengths at those standard body lengths are set forth in Table 14.

TABLE 14

Amphisbaena fuliginosa — Tail length at certain body lengths, as calculated from the regression line, in the basic samples.

Locality	*Body length — mm*			
	110	*250*	*350*	*400*
Manaus	16.9	32.8	44.2	50.0
Colombia	17.9	37.7	51.9	59.0
Panama	16.7	37.0	51.5	58.8
Iquitos	19.3	43.1	60.1	68.6
Ucayali River	16.5	40.7	58.0	66.7
Ecuador	13.2	38.0	55.7	64.5
N. British Guiana	19.4	35.2	46.5	52.1
Dutch Guiana	18.2	37.5	51.3	58.2
Trinidad	7.8	38.2	59.9	70.8

The first type of comparison to be made is between samples belonging to the same group of *b* values. These comparisons are shown in Table 15.

TABLE 15

Amphisbaena fuliginosa — Comparison of tail lengths at standard body lengths in different pairs of samples having similar values of the coefficient of regression *b*.

Pairs of samples	*Body length — mm.*			
	110	*250*	*350*	*400*
Manaus (0.114) N. British Guiana (0.113)	+++	–	–	–
Colombia (0.142) Panama (0.145)	+++	–	–	–
Colombia (0.142) Dutch Guiana (0.138)	–	–	–	–
Panama (0.145) Dutch Guiana (0.138)	++	–	–	–
Iquitos (0.170) Ucayali River (0.173)	++++	–	–	–
Iquitos (0.170) Ecuador (0.177)	++++	++++	+	–
Ucayali River (0.173) Ecuador (0.177)	++++	–	–	–

In this and similar tables

—	means a probability larger than 0.05 of the differences being due to random fluctuations;
+	probabilities equal to or smaller than 0.05 and larger than 0.02;
+ +	probabilities equal to or smaller than 0.02 and larger than 0.01;
+ + +	probabilities equal to or smaller than 0.01 and larger than 0.001;
+ + + +	probabilities equal to or smaller than 0.001.

Although all pairs but one differ at birth, it is obvious that they converge toward the same tail length at adult age.

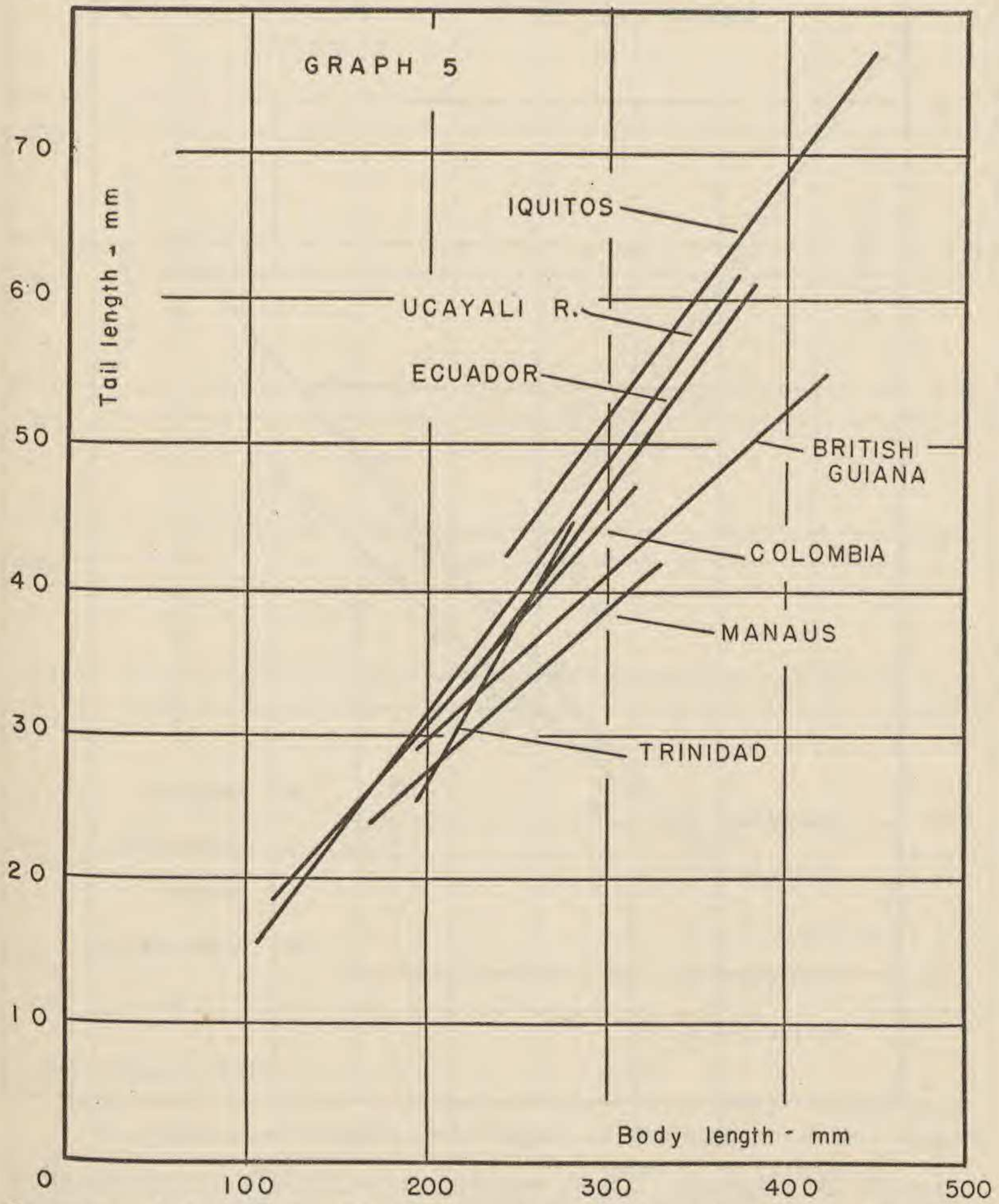
Comparing samples belonging to different groups of *b* values (Table 16) we see that the situation here is different. Differences arise where they did not exist at birth, or remain significant when they were so at birth. The only, and very interesting, convergence is that between Trinidad and Iquitos (naturally repeated for Trinidad and Ucayali and Ecuador). This tends to show that the differences in *b* really have no significance in this case. It should be added that the values for young specimens from Trinidad (extrapolated, as the smallest observed measures 195 mm body length) are so small that it is to be expected that the finding of newly born individuals will change either the slope or the form of the regression curve.

TABLE 16

Amphisbaena fuliginosa — Comparison of tail lengths at standard body lengths in different pairs of samples having dissimilar values of the regression coefficient *b*.

Pairs of samples	*Body length — mm.*			
	110	*250*	*350*	*400*
Manaus (0.114) Colombia (0.142)	+	++++	++++	++++
Manaus (0.114) Iquitos (0.170)	++++	++++	++++	++++
Manaus (0.114) Trinidad (0.217)	++++	++++	++++	++++
Manaus (0.114) Dutch Guiana (0.138)	++	++++	++++	++++
N. British Guiana (0.113) Trinidad (0.217)	++++	+++	++++	++++
N. British Guiana (0.113) Dutch Guiana (0.138)	–	–	+	+++
Colombia (0.142) Trinidad (0.217)	++++	–	++++	++++
Colombia (0.142) N. British Guiana (0.113)	++	+	+++	++++
Trinidad (0.217) Iquitos (0.170)	++++	++++	–	–

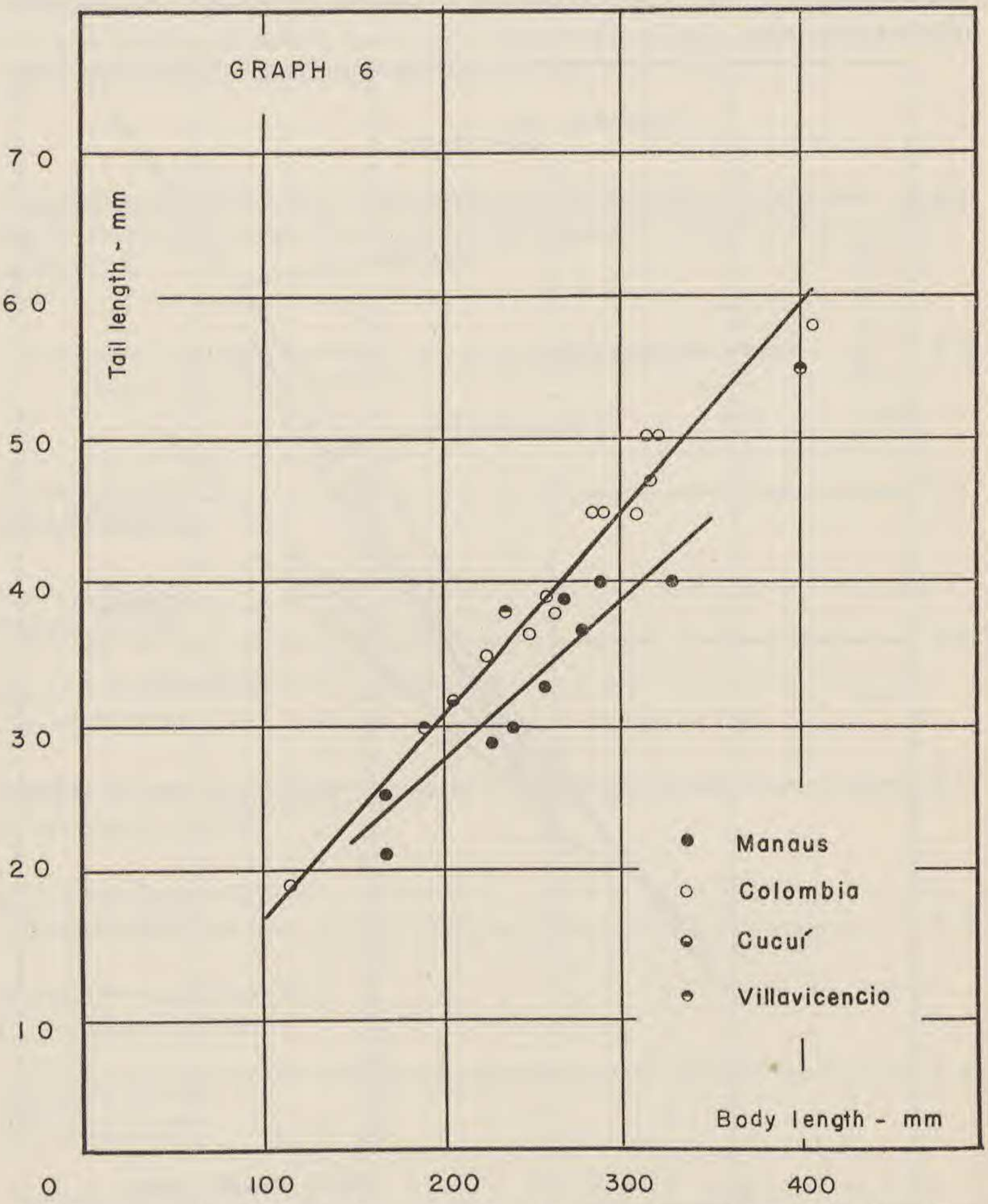
Turning now to the geographical features of the variation in tail length, we see that the Iquitos-Ucayali assemblage constitutes a fairly natural group. The relationship of Trinidad to this group may be explained in one of two ways: either all belong to the same population of tail lengths (which would occupy a large belt separating Manaus-British Guiana from Colombia-Panama) or we are facing a case of parallelism. It will be seen that the former hypothesis seems more likely to be true.



Graph 5. *A. fuliginosa.* Linear regression of tail length on body length for the fundamental samples. Samples from Panama and Dutch Guiana omitted on account of overlapping almost completely with Colombian sample.

The Manaus-British Guiana group and the Colombia-Panama ones are also very natural. Dutch Guiana, resembling the latter, must be a case of parallelism.

Graph 5 shows pictorially the relationships between these groups. Panama and Dutch Guiana are omitted because they virtually overlap Colombia.

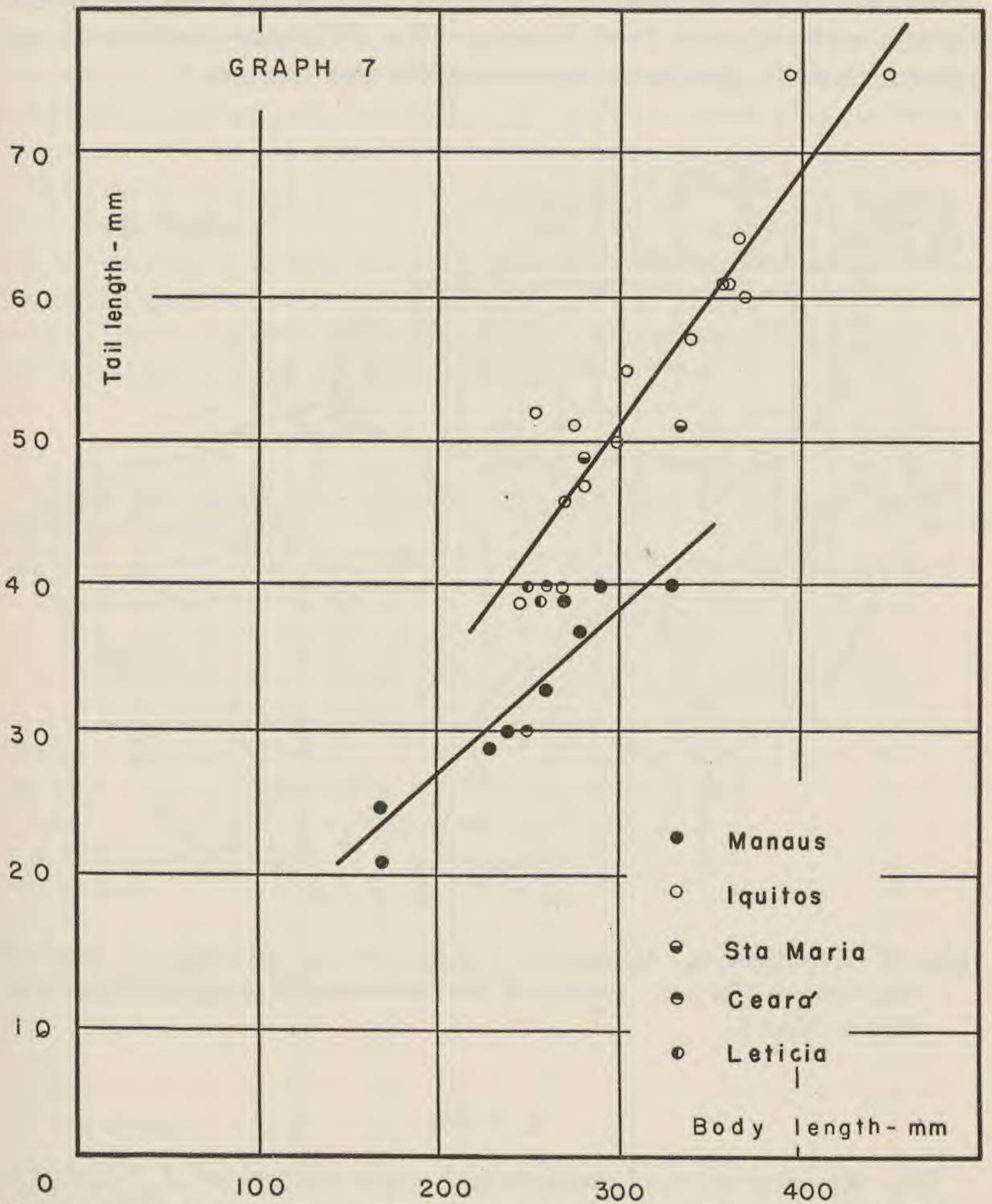


Graph 6. *A. fuliginosa.* Linear regression of tail length on body length in the samples from Manaus and Colombian Andes, showing actual points for visual evaluation of goodness of fit and comparison of specimens from intervening territory.

Considering now the specimens not included in the above discussion, we find that Cucuí and Villavicencio tend strongly toward the Colombian side (Graph 6) instead of the Amazonian.

Leticia (Graph 7) shows a position really intermediate between Manaus and Iquitos. A similar relationship exists in the case of Vista Alegre and Marudi River, between Manaus and British Guiana.

The material from eastern Brasil (Santa Maria) shows decided dis-

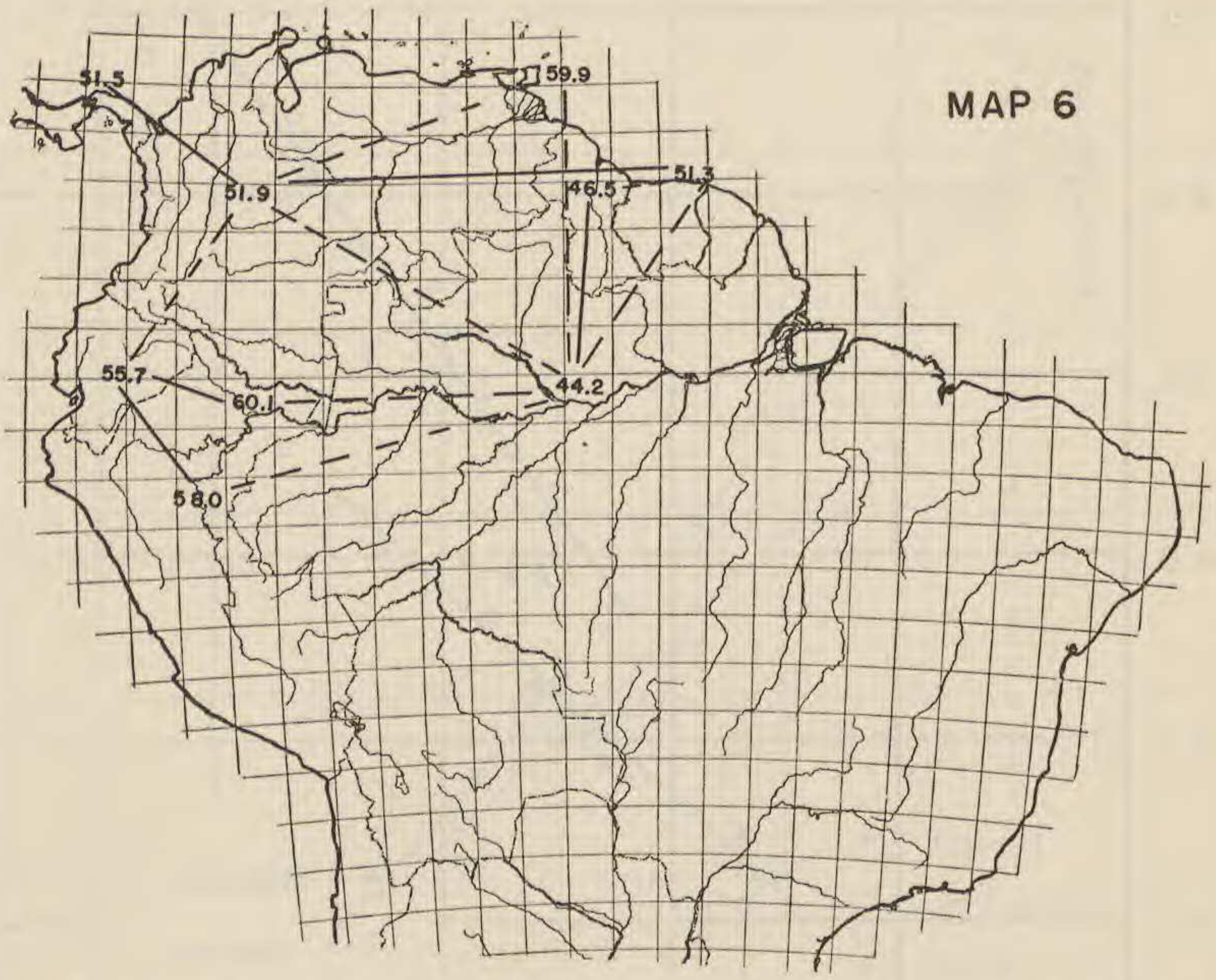


Graph 7. *A. fuliginosa.* Linear regression of tail length on body length in the samples from Manaus and Iquitos, showing actual points for visual evaluation of goodness of fit and comparison of specimens from other localities.

agreement with that from Manaus, once more. This does not happen in the case of Ceará (Graph 7).

Thus the general picture of tail length differentiation seems to be the following:

A short-tailed population is present in the Amazon valley and British Guiana. Long-tailed populations are present in the region from the Ucayali River and Iquitos up to the Pacific coast of Ecuador and Trinidad. Populations with intermediate values are found in Dutch Guiana and Colombia and Panama. The differences considered are present in adult specimens, measuring 250 mm or more.



Map 6. *A. fuliginosa.* Geographic variation of the tail length at standard body length 350 mm. Values for the basic samples shown. See also caption to Map 2.

6. Color

The characteristic and unmistakable color pattern of *A. fuliginosa,* described by Linné in the Systema Naturae as "alba, ex atro fusco varia, capite immaculato" and by Boulenger (1885: 438) as "Black and white, either the one or the other color predominating" can be reduced to four elements that seem to vary with a certain degree of independence in the material examined.

These elements are:

a. the ground color;
b. the spotting of the head;
c. the dorsal pattern and
d. the ventral pattern.

In the following discussion the color patterns will be considered as seen in not badly faded alcoholic specimens. I believe that the utility of taxonomic characters only observable in live or freshly killed animals is limited to giving more authority, by positive correlation, to other characters observed in regularly preserved museum specimens.

The ground color of *A. fuliginosa* shows two extremes: a very light, whitish yellow (figs. 2, 3, 4, 7, 9, 10, 11) and a dirty, grayish pink (figs. 5, 6, 8). On the first type the dark spots have precise margins; on the second the spots are rather smudgy, especially on the head. Difference between the two phases can be judged by comparison of figs. 7 and 8, of two specimens from Riobamba, Ecuador.

TABLE 17

Amphisbaena fuliginosa — Number of specimens with different ground colors in several samples.

Locality	*Ground color*			
	Yellow	*Intermediate*	*Dirty pinkish*	*Total*
Panama	—	—	10	10
Colombia	1	3	10	14
Trinidad	4	12	—	16
N. British Guiana	6	—	—	6
Villavicencio	—	1	3	4
Cucuí	1	2	—	3
Manaus	10	—	—	10
Ecuadorian Andes	4	2	1	7
Daule River	—	—	1	1
Bucay	—	—	1	1
Luoula	2	—	—	2
Santiago River	1	—	—	1
Avila	1	—	—	1
Pastaza River	1	—	—	1
Cenipa River	1	—	—	1
Iquitos	18	—	—	18
Ucayali River	10	—	—	10

The yellow ground color is the only one found in Brasil, the Upper Amazon and the Guianas. Conversely, the smudgy phase is the only one found in Panama. In Colombia we have almost complete predominance of the smudgy form; in Trinidad and Ecuador the composition of the samples is transitional (Table 17).

The smudgy form presents very little variation of the remaining color elements. The head spots are generally multiple, small, with rather indistinct margins. The belly has usually the same amount of black as the dorsum. When the head is sparsely spotted, it presents a characteristically dirty pinkish color. (fig. 5).

In the yellow form we have considerable variation of the rest of the pattern.

The head varies from immaculate to heavily spotted. In Manaus immaculate heads are found almost exclusively. In Paramaribo the heads are a little more spotted. In British Guiana there is a majority of spotted heads and the same holds true for Trinidad. In Iquitos the proportion of spotted heads is also very high, much more so than in the Ucayali. The Ecuadorian material agrees rather with the latter. In the Brasilian samples only one spotted head (with a single very small spot) was found. These data are summarized in Table 18.

TABLE 18

Amphisbaena fuliginosa — Number of specimens with immaculate and spotted heads in several samples.

Locality	*Head pattern*		
	Immaculate	*Spotted*	*Total*
Manaus	9	1	10
Leticia	–	3	3
Iquitos	2	16	18
Ucayali River	5	5	10
Ecuador	4	3	7
Vista Alegre	1	–	1
Marudi River	–	1	1
N. British Guiana	1	5	6
Trinidad	1	15	16
Paramaribo	4	2	6
Ceará	2	1	3
Santa Maria	2	1	3

Analysis permits us to conclude that among the population with a clear yellowish ground color a differentiation in color pattern is found. A form with very little spotting is found from Manaus east and south to Baía. In the rest of the territory there is a variable but always large amount of head spotting.

The dorsal pattern presents a very interesting variation. A minimum amount of black is found in Iquitos, Ucayali River and some of the Ecuadorian specimens (the ones with the yellow ground color). The dorsal spots here form narrow, irregular, transverse bands, prolonged down the flanks to the sides but not across the abdomen, which is lighter than the back (figs. 7, 11).

In Manaus, Dutch Guiana, British Guiana and, partially, Trinidad the dark spotting is much heavier, with a tendency in the Guianas to a "polka dot" pattern, with yellowish dots on a black or very dark brown dorsum. Here also the abdominal pattern is much lighter. (figs. 2, 3, 4).

The most melanistic form is that found in Santa Maria. Here even the abdomen is almost completely dark. The Ceará specimens are similar to the Manaus - Guianas ones, but for one (IB 681 A) that could be mistaken for one of those from Santa Maria.

Integrating these data into a general pattern we find:

In Panama and Colombia there is a form with a dirty pinkish ground color and smudgy darker spots evenly distributed on back and belly (figs. 5, 6).

In Manaus we find a form with a very light yellow ground color, the head immaculate, the body with dark spots having very distinct margins, more concentrated in the front part of the dorsum and much scarcer on the abdomen. Intergradation between these two forms is found in Cucuí and Villavicencio. These intergrades present either an intermediate ground color or a very definite Colombian pattern; only one of them has an immaculate head.

In Dutch Guiana (fig. 2) we find a form much like the Manaus one; the most sensible difference is the larger amount of spotted heads.

In British Guiana a form is found with an even larger proportion of spotted heads. In Trinidad there is definite evidence of intergradation between populations in British Guiana and Colombia. The ground color is decidedly intermediate but the spots are not smudgy: they tend to the pattern found in British Guiana. Another intergrade is the Riocito specimen.

In Leticia we find the Manaus form intergrading with another one (fig. 11) that occupies the Ucayali River valley up to Iquitos. Here there is the same spotting of the head seen in the sample from British Guiana, although the proportions differ. The ground color is the same.

But the dorsal pattern is different, with a tendency toward reduction of the amount of black and formation of narrow irregular transverse bands; the abdomen is much lighter. This form intergrades with the Colombian one in Ecuador. The Upper Amazonian specimens, up to the foothills of the Andes, agree entirely with the lowland material. In Riobamba (figs. 7, 8) one specimen clearly belongs to the Colombian form and two are somewhat intermediate.

Finally we find in Santa Maria a very distinctive form (figs. 9, 10) with yellow ground color and with the dorsum and abdomen almost solidly dark.

Geographical differentiation: synthesis

After presenting detailed accounts of the variation of single characters in the territory studied, let us try to take a panoramic view of the geographic differentiation of *A. fuliginosa*. This problem presents two aspects: (a) the analysis of the total similarity and divergence among the several samples; (b) the feasibility of identifying single specimens.

With regard to the first aspect, the question that at once arises is one of method. Klauber (1943 a) has discussed the problem with his usual thoroughness and ability. In this case, however, very little advantage would result from the application of his methods; the best understanding of the situation seems to me to result from the consideration of the data presented above with no further elaboration.

In the series of small tables presented below a plus sign implies a statistically significant difference; a minus sign a not significant one.

No two samples agree in all characters. This is by no means a novel observation, as pointed out by Mayr (1947: 34) and Simpson (1947: 201), but its bearing on strictly taxonomic (or rather nomenclatorial) problems has been somewhat underestimated by herpetologists, leading to the erection of what seems to me a larger number of new names than the small amount of evidence warrants.

The best agreement between samples is found between Colombia and Panama (Table 19). They agree very closely in number of body and tail annuli, dorsal and ventral segments, tail length at adult size and general color pattern. The only difference is in the number of preanal pores. In this character the means are uniform throughout the range, with the exception only of Colombia and Trinidad. This is a common phenomenon and more logically to be expected than concomitant variation of all characters.

Turning now to a consideration of the relationships of the Colombian material to the neighboring samples, it is pertinent to note in the first

TABLE 19

Amphisbaena fuliginosa — Summary of the differences between the sample from the Colombian Andes and several others.

Characters	*Samples*			
	Panama	*Trinidad*	*Ecuadorian Andes*	*Manaus*
Body annuli	−	+	+	+
Tail annuli	−	+	+	+
Dorsal segments	−	−	−	+
Ventral segments	−	−	−	+
Preanal pores	+	−	+	+
Tail length at body length 400 mm	−	+	+	+
Color	−	±	±	+

place the homogeneity of all the Colombian specimens, excluding only Villavicencio and including the Venezuelan locality of Riocito.

Taking Trinidad first (Table 19) we see agreement in the number of dorsal and ventral segments and in the number of preanal pores. The number of segments has no great significance in this case, as a glance at Map 3 shows immediately. The number of pores is important, because it is a strikingly aberrant character shared only by these two samples from adjoining regions. On the other hand, in number of tail annuli the difference between Colombia and Trinidad is significant. In number of body and tail annuli the Trinidad sample agrees with that from northern British Guiana; in number of pores and color it is intermediate. The three samples disagree in relative tail length.

If we take the material from Trinidad to represent the adjacent mainland, we can conclude that between British Guianan and Colombian material there is a difference of subspecific rank and that intergradation occurs in Venezuela. Investigations of this intergradation and of the real relationships between the forms inhabiting the continent and Trinidad are among the most interesting to be undertaken when adequate material is available.

Let us compare now the Colombian material with the Ecuadorian and Upper Amazonian samples. It is easy to see that the differences between Colombia and Iquitos are numerous and sharp. The only agreement is in the rather unimportant matter of segments, which do not vary in the occidental part of the range. Ecuador is a region of intergradation, where we find either intermediate specimens or examples attributable to each of the two forms living side by side.

To complete the analysis of this Colombian subspecies, the differences between Colombia and Manaus remain to be examined. These differences are highly significant for all characters. Furthermore, the small samples from Cucuí and Villavicencio show intergradation, and I believe it to be safe to conclude that one subspecies of *Amphisbaena fuliginosa* occupies the highlands of Colombia, reaching the Pacific Ocean to the West, the Isthmus of Panama and the northwest coast of Venezuela to the north. The hardest problem connected with this form (besides intergradation in Venezuela) is the feature of intergradation in the region north of Iquitos and south of Villavicencio.

TABLE 20

Amphisbaena fuliginosa — Summary of the differences between the sample from the Ucayali River and several others.

Characters	*Samples*		
	Iquitos	*Ecuadorian Andes*	*Manaus*
Body annuli	+	+	+
Tail annuli	–	+	+
Dorsal segments	–	–	+
Ventral segments	+	+	+
Preanal pores	–	–	–
Tail length at body length 400 mm.	–	–	+
Color	–	±	–

The Ucayali River valley and the Iquitos samples present almost the same degree of agreement as the Colombian and Panamanian ones (Table 20). Disagreement here is with respect to two characters: number of body annuli and number of ventral segments. The difference in number of ventral segments has probably the same meaning as in number of pores in Colombia and Trinidad samples. The difference in number of body annuli, however, has a more important meaning. The Iquitos sample is intermediate between that from the Ucayali and that from Ecuador, but not that from Manaus. The Leticia sample, geographically closer to Iquitos, agrees more with the sample from Manaus and does not even approach the values found in Iquitos (see

Map 2). Rather peculiar also is the circumstance that in tail annuli and tail length Iquitos presents higher values than Manaus, Ecuador, Ucayali River and Colombia. These puzzling features seem to be due to local differentiation coupled with subspecific hybridization.

The differences between Manaus and Iquitos are decidedly significant (Table 21).

We may then safely conclude that a subspecies of *A. fuliginosa* occupies the Ucayali River valley up to Iquitos on the Amazon, intergrading in Ecuador with the Colombian subspecies and in the Leticia region with a middle Amazonic subspecies. As has already been noted, critical material for the understanding of this form must be collected in the region to the north of Iquitos, east of the Ucayali (region of the rivers Javarí, Juruá and Purús) and down the Amazon to Manaus.

TABLE 21

Amphisbaena fuliginosa — Summary of the differences between the sample from Manaus and several others.

Characters	*Samples*		
	Iquitos	*British Guiana*	*Dutch Guiana*
Body annuli	+	+	+
Tail annuli	+	–	–
Dorsal segments	+	+	–
Ventral segments	+	–	–
Preanal pores	–	–	–
Tail length at body length 400 mm.	+	–	+
Color	–	–	–

Turning now to the northern coast of South America, we have already discussed the relationships among Colombia, Trinidad and British Guiana. Lack of Venezuelan material makes it inadvisable to compare Trinidad with Manaus, but a comparison must be made between the latter and the British Guianan material (Table 22).

The chief differences between the above mentioned samples are in color and number of body annuli. Agreement is present in number of tail annuli and proportional tail length. Inasmuch as Manaus presents a very homogeneous and distinct sample, I think it wise to separate the British Guianan population subspecifically from the middle Amazonian one. The upper Branco River is in all probability the zone of intergradation, as indicated by the specimens from Marudi River and Vista Alegre.

The Dutch Guiana population should, at least for the time being, be included in this British Guianan subspecies. Its relationships to Manaus in dorsal segments and color tend to show that its differentiation has been achieved in a probably independent way from British Guiana populations. The same is indicated by the sharp differentiation in tail length.

The paucity of material, however, makes it wiser to keep the populations of Dutch Guiana, British Guiana and Trinidad lumped under one subspecific name. Collection of more material, especially from Venezuela, French Guiana and Pará, will eventually modify this *status quo*, but it seems to me better to split in the future a composite form than to risk the addition of new synonyms to an already overburdened taxonomy.

TABLE 22

Amphisbaena fuliginosa — Summary of the differences between the sample from British Guiana and the remaining samples from northern South America.

Characters	*Samples*	
	Trinidad	*Dutch Guiana*
Body annuli	−	−
Tail annuli	−	−
Dorsal segments	−	−
Ventral segments	−	−
Preanal pores	+	−
Tail length at body length 400 mm.	+	+
Color	±	−

The small sample from the State of Ceará agrees rather well with the Manaus sample, but shows a tendency toward a lower number of body annuli and toward the type of coloration found in Santa Maria. So we may include this region in the area occupied by the middle Amazonian population, keeping in mind a probable intergradation with an eastern Brasilian form.

This eastern Brasilian form is represented by the three specimens from Santa Maria.

It is curious and sad that these three specimens, the only ones known from the region, as far as I am informed, were collected by Maximilian

TABLE 23

Synopsis of the races of *A. fuliginosa*

	fuliginosa	*amazonica*	*varia*	*bassleri*	*wiedi*
Body annuli	196–213	207–221	190–205	204–215	197–206
Tail annuli	24–28	24–27	23–27	26–30	24–28
Segments on a mid-body annulus	20–28/20–28	22–26/22–26	20–26/20–26	20–22/18–24	26/24–26
Pores	6–10	8–9	6–9	6–8	8–10
Ground color	Yellow	Yellow	Dirty pinkish	Yellow	Yellow
Head	Immaculate or spotted	Immaculate (rarely spotted)	Smudged	or spotted (rarely immaculate)	Immaculate
Dorsal pattern	Dense black markings, tending to a checkered pattern	Dense black markings	Smudgy, very dense	Sparse, tending toward formation of transverse irregular bands	Extremely dense
Ventral pattern	Similar to dorsal, but much lighter	Similar to dorsal but lesser amount of black	Almost as dense as dorsal	Almost immaculate	Similar to dorsal
Tail length at body—length 400 mm.	*	50.0 mm	59.0	67.5	**
Distribution	Guianas, Trinidad, Venezuela	Middle Amazon	Uplands and Pacific coast of Colombia, Panama	Ucayali River valley	Santa Maria, State of Baía, Brasil

* Too variable within the range.
** Too few specimens.

more than a hundred years ago. I have seen the excellent collections assembled by Ernesto Garbe for the Museu Paulista in the same region, including, for instance, the rare *Amphisbaena leucocephala* Peters, a new species allied to *A. steindachneri*, etc., and not a single specimen of *A. fuliginosa*. There are, however, reasons to believe that the species really exists or has existed in the region of Ilheus. There is a close relationship between the fauna of the humid forest of eastern Brasil and the Amazonian fauna, from which the former is separated by a broad belt of savanna with diverse faunal composition. This fact will receive more attention in connection with the mode of evolution of *A. fuliginosa*.

If we accept the locality data of the three Maximilian specimens, as I see no reason for not doing, it is necessary to give them subspecific rank, as the differences from the other samples are numerous and striking.

We have in this way considered five subspecies of *A. fuliginosa*. The validity of these races does not depend solely on the demonstration of statistical differences but, also, on the possibility of identifying isolated specimens in the museum. Nomenclature was never intended to, nor can it, describe the great complexity of evolutionary patterns. In groups, such as *Peromyscus*, intensively worked from an evolutionary viewpoint, a compromise has been reached between the need of acknowledging through the name morphological differences and the unreasonable splitting that results from too strict an adherence to the statistical significance of differences.

The five races here recognized are listed in Table 23 which will serve as differential diagnosis for all. The names under which they appear have been assigned for reasons discussed below.

Specimens of *varia* are easy to identify, on account of the very characteristic color pattern and low number of body annuli.

Among the forms with yellow ground color, *bassleri* and *wiedi* are easy to recognize with the aid of the dorsal pattern and additional characters, such as number of tail annuli in *bassleri*.

The subspecies *amazonica* is readily identifiable by the combination of high body annuli counts and immaculate head. There is some overlap with *bassleri* and *fuliginosa*. The subsidiary characters, however, permit a good separation.

To my way of thinking, the hardest separation is between *bassleri* and *fuliginosa*, dependent on color pattern and number of tail annuli, a character not always present and not too sharply diagnostic. But here again the ancillary characters (chiefly number of pores and segments) afford good elements for separation.

Mode of evolution of *A. fuliginosa*

In taxonomic discussions of evolutionary patterns a prominent place is usually given to the identification and discussion of "centers of dispersal". Several rules and "laws" have been advanced for that purpose. In the case of South American forms I believe a different attitude to be more fruitful: instead of looking for centers of distribution, to consider only the modifications of the probable Pleistocene ranges of the form or forms involved. In the case of forms that entered South America during the Pliocene, there is of course a secondary center of dispersal to be considered — the Isthmus of Panama. But even in the elucidation of the history of such genera including species outside of South America the concept of centers of dispersal seems to me rather unsatisfactory. Perhaps the most, if not the only, legitimate application of such a concept would be in the case of forms existing in areas submitted to glaciation and temporarily restricted to refuges. This does not seem to be the case with any of the reptiles and amphibians that entered South America through the Isthmus of Panama.

Before beginning a discussion of the origin and meaning of the observed distribution of *A. fuliginosa*, some preliminary considerations must be undertaken.

A. fuliginosa is most certainly a very ancient inhabitant of South America. It is not an "Old Northern" element (Dunn, 1931) but an indigenous one. No evidence is available as to the geological age of the species or even the genus. The North American genus *Rhineura* is present in the Oligocene of the United States, and I should think *Amphisbaena* is at least as old. What seems to me indirect proof of the antiquity of *Amphisbaena* is the existence in Africa of some species closely related to the South American ones.

Another remark concerns the abundance of *A. fuliginosa*. From the data gathered on the occurrence of the species of *Amphisbaena* it seems that the relative frequency of *A. fuliginosa* varies from one part of the range to another. This relative frequency would be maximum in northwestern South America and minimum in the Brasilian territory outside the Amazon valley. Such variations in abundance are in most forms ascribable to accidents of sampling, especially in the case of subterranean forms. *A. fuliginosa*, however, has been collected since pre-Linnean days with about the same relative frequency and I believe the data above reflect the true situation.

Another remark concerns the limitations of this study. I have little or no material from vast and important areas in Venezuela, French Guiana, the whole lower Amazon and most of the Brasilian territory and the Peruvian Andes.

With these remarks in mind, let us analyze the evolutive features of the distribution of *A. fuliginosa.*

Several of the characters investigated have a "checkerboard" type of distribution; such are the number of segments and pores, the number of tail annuli and the tail length.

This type of differentiation can result either from non-adaptive evolution or from adaptation to very specialized conditions. I can imagine two of those characters as being directly adaptive: the tail length and the number of segments.

The tail length might be of adaptive value in relation to predation. The chief predators of the amphisbaenids are the coral snakes of the genus *Micrurus,* that are frequently collected while swallowing or soon after having swallowed amphisbaenids. I suspect this is the adaptive explanation of an optimum point of fracture in the tail; this point of fracture is present not only in *Amphisbaena* but also in *Aulura,* a genus of leposternoid affinities. I can conceive there would be some advantage in the dropping of a longer tail in the mouth of a hungry pursuer.

Also in connection with predation could be found a direct adaptive value of the increase in number of segments to a midbody annulus. If this number of segments corresponds to the girth, it is reasonable to suppose that an animal with more segments, i.e., thicker, would be harder to prey upon. But our data do not permit us to check on the relationship between number of segments and girth and so these considerations are, for the moment, pointless.

Turning now to the consideration of the color pattern and of the number of body annuli, we find a more interesting picture.

These two characters vary almost parallelly. One might assume that they are either determined by pleiotropic genes or linked. The first hypothesis is improbable, for such a complex color pattern is probably determined by a complex genetic mechanism. The hypothesis of linkage may be dismissed by the observation of specimens presenting contrasting values of the two varieties (*A. f. varia* x *A. f. bassleri,* for instance). I believe this parallel variation of unlinked characters speaks strongly in favor of an adaptive factor in their evolution.

The discussion of the evolutive pattern of *A. fuliginosa* centers around three subspecies: *fuliginosa, bassleri* and *amazonica. A. f. varia* is undoubtedly a highland form that reached the Pacific coast. *A. f. wiedi* is probably a disjunct form and as such will be discussed.

Considering now the three above cited species, we may say that, although *A. f. amazonica* has a range situated between those of *bassleri* and *fuliginosa,* its characteristics are not intermediate between those of the named forms. On the contrary, *bassleri* and *fuliginosa* are very closely related forms, differing chiefly in color.

This situation could have arisen in two ways: (a) *amazonica* giving rise to two convergent forms in different parts of the range; (b) *amazonica* being the result of the evolution of a population occupying the central part of a territory, on the fringes of which the primitive stock suffered further but less extreme differentiation.

If we consider now *varia* and *wiedi* we see that they approach more closely the forms with low counts of body annuli (*bassleri* and *fuliginosa*) than *amazonica*. In this manner I believe the second hypothesis listed above is the more probable, and that *fuliginosa* and *wiedi* are closer to the primitive stock than any other race. From the data furnished by the color pattern it would seem that *fuliginosa* is still closer to the parental stock than *wiedi*, but the elements at present available do not warrant investigation of this point.

If the presence of *varia* is easily accounted for, *wiedi* offers a difficult problem. It is one more instance of an eastern Brasilian representative of the Amazonian fauna. Many examples of this peculiar duplication are found in lizards (*Anolis*, *Enyalioides*), snakes (*Leptotyphlops*, *Boa*, *Lachesis*), amphibians (Carvalho, 1946), birds (*Cotingidae*, p. ex. — O. Pinto *in litt.*), mammals (Moojen, 1948) and certainly many other groups.

Moojen's explanation of the fact is sensible and may be summarized here by assuming that central Brasil was covered during the Pleistocene by a tropical forest which vanished before recent times. The causes of this recession are many and need not be discussed here. In our day the humid eastern Brasilian forest, which covers a broad coastal belt from Baia to the northern part of Rio de Janeiro, is separated from the Amazon forest by a stretch of savanna. It is thus perfectly understandable that forms which need a humid environment have become isolated in eastern Brasil from the northern populations. In the case of *A. fuliginosa*, however, if we may feel reasonably sure that a central Brasilian population once existed, there is no need to assume that it is now extinct, for we have three specimens from Ceará, a generally dry state.

The presence of *A. fuliginosa* in northeastern Brasil suggests furthermore an alternative origin for the eastern Brasilian form: migration through the coastal "matas". Discontinuity of suitable environments along this route, however, militates against this mode of origin.

More elements for the solution of this problem would be afforded by a consideration of the relationships of *A. f. wiedi*. The evidence at hand points immediately to a closer relationship to the forms *bassleri* and *fuliginosa*. This may mean either derivation from the primitive stock, which the cited races probably resemble more closely than the remainder, or derivation from one of the two.

A. f. bassleri is so specialized with respect to color that it is unlikely to be a parental form, a role whose requirements are better fulfilled by *fuliginosa*. However, in order to accept *wiedi* as derived from *fuliginosa* by migration, it is necessary that the latter form be found in the lower Amazon. So far we have no evidence either for or against this hypothesis. The material from Ceará and Maranhão, however, seem to indicate that perhaps *amazonica* will be found in Pará and northeastern Maranhão.

This is a problem that will only be settled when adequate material is collected all over the Brasilian range of *A. fuliginosa*.

To summarize the whole argument on the distributional pattern of *A. fuliginosa*, I think it is safe to state that:

The Pleistocene range of the species probably included central Brasil and the Amazon valley up to the Guianas.

Around the Amazon valley three forms evolved: *amazonica*, in the Manaus region, characterized by very high body annuli counts and an immaculate head; *bassleri*, along the Ucayali River valley up to the upper Madre de Dios, presenting a strong differentiation of color pattern and an increase in tail length; *fuliginosa* in the Guianas and Venezuela, showing an increase in number of body segments and preanal pores and preserving many characteristics of the ancestral form. It is possible that differentiation in this region proceeded further and that the present status will be modified.

The primitive amazonic population climbed the Andes, probably before full differentiation of the lowland races; the highland population, extending its range west to the Pacific Ocean and north to the Isthmus of Panama, suffered a striking differentiation of color pattern and a reduction in the number of body annuli.

The mode of origin of the presently disjunct *A. f. wiedi* awaits more adequate data that will permit a satisfactory solution.

The belts of intergradation are very wide, and there seems to be no noticeable restriction of gene flow between the races.

Attribution of names

Amphisbaena fuliginosa is included in the tenth edition of the Systema Naturae. The diagnosis is, of course, very short, but reference is made to two of Linné's previous works.

Linné makes reference in the Systema to two specimens; the pre-Linnean references, however, concern just one of the two. This is described in "Amoenitates Academicae" (1749 **1**: 295) among others belonging to the "Museum Adolpho Fridericianum", more commonly known as "Museum Principis". To this description reference is made in the "Museum Adolphi Friderici Regis" (1754). Of this specimen, preserved in the Royal Museum in Stockholm, I have been supplied with very good photographs and other data, thanks to the kindness of Dr. U. Bergström.

The second specimen is described in another part of the Amoenitates, the "Surinamensia grilliana" (1749a). This book is not cited in the Systema Naturae, but the data on the specimen are. A fine series of photographs of this second cotype, preserved in the Zoological Institute at Uppsala, was made available to me, together with other numerical data, by Dr. Åke Holm.

TABLE 24

A. fuliginosa — Characteristics of the two Linnean cotypes.

Character	Specimen from	
	Uppsala	*Stockholm*
Body annuli	205	208
Tail annuli	25	28
Dorsal segments	30	23
Ventral segments	26	26
Preanal pores	10	8
Body and tail length	455+64 mm.	310+45 mm.

In Table 24 are presented the numerical characteristics of these Linnean cotypes.

We shall try to determine the probable origin of these Linnean cotypes.

The Stockholm specimen

The color pattern of the Stockholm specimen, perfectly preserved (fig. 1), belongs to the type found in the Guianas and Manaus.

The number of body annuli (208) would fit well into the Guianan samples (199–213), into the Ucayali race (205–215) and less well into the Manaus race (207–221). (Table 2)

The number of tail annuli (28) would also fit into the Guianan (24–28) and Ucayali (26–30) races. (Table 23)

The number of dorsal segments (23) could belong to any sample, with the possible exception of the Ucayali River one. (Table 9)

The number of ventral annuli (26) points clearly to the Guianas and Manaus. (Table 9)

The number of preanal pores (8) is absolutely nondiagnostic. (Table 10)

The tail length fits best of all the Paramaribo sample, and excludes the Ucayali River race. (Table 12)

On the strength of these data it seems justifiable to believe that the Stockholm cotype of *A. fuliginosa* was collected somewhere in the Guianas.

TABLE 25

A. fuliginosa — Stockholm cotype. Probability of the differences between the observed values for the specimen and the means of the listed samples being due to random variation inside a homogeneous population.

Samples	*Body annuli*	*Tail annuli*	*Dorsal segments*	*Ventral segments*	*Tail length*
Manaus	0.20	0.85	1.00	0.10	0.10
Colombia	0.04	0.57	0.40	0.09	0.60
Panama	0.06	0.70	0.35	0.011	0.24
Iquitos	0.91	0.010	0.014	0.001	0.05
Ucayali	0.50	0.042	0.021	0.011	0.13
Ecuador	0.11	0.74	0.037	0.001	0.65
British Guiana	0.69	0.84	0.16	0.09	0.38
Paramaribo	0.34	0.44	0.44	0.17	0.80
Trinidad	0.57	0.63	0.08	0.07	0.014

TABLE 26

A. fuliginosa — Uppsala cotype. Probability of the differences between the observed values for the specimen and the means of the listed samples being due to random variation inside a homogenous population.

Samples	*Body annuli*	*Tail annuli*	*Dorsal segments*	*Ventral segments*	*Preanal pores*	*Tail length*
Manaus	0.07	0.10	0.001	0.10	0.030	0.13
Colombia	0.10	0.012	0.005	0.09	0.028	0.42
Panama	0.17	0.08	0.001	0.011	0.09	0.020
Iquitos	0.32	0.76	0.001	0.001	0.001	0.030
Ucayali	0.15	0.94	0.001	0.011	0.012	0.036
Ecuador	0.39	0.38	0.001	0.001	0.051	0.09
British Guiana	0.84	0.026	0.001	0.09	0.10	0.026
Paramaribo	0.70	0.10	0.010	0.17	0.15	0.70
Trinidad	0.66	0.043	0.001	0.07	0.014	0.001

The Uppsala specimen

The Uppsala specimen, although apparently normally colored when examined by Linné, is today extremely faded and no elements can be gathered from its color pattern.

The number of body annuli (205) agrees with the Guianan and Ucayalian races, and with no other. (Table 2)

The number of tail annuli (25) may well belong to any sample but the Ucayali one. (Table 7)

The number of dorsal segments is extremely high, higher than any recorded by me. If this is not the product of different methods of counting, it constitutes the highest number for the species. Even so, the only race that closely approaches such a high value is the one from the Guianas (20-28). (Table 8)

The number of ventral segments (26) also agrees with the Guianan samples, and others (all but the Ucayali River race).

The number of preanal pores (10) is characteristic of the Guianan (Dutch Guiana) and eastern Brasilian races. (Table 10)

Finally, the relative tail length is similar to that found in the Dutch Guiana and the Colombia races. (Table 12)

It is a safe conclusion to say that this specimen also is probably originally from the Guianas, more probably Dutch Guiana.

The data above justify me in applying the name *fuliginosa fuliginosa* to the form that inhabits the Guianas and, more specifically, Dutch Guiana, an assignment in conformity with what we know of the origin of the Linnean types.

Laurenti (1768) abandoned the name *fuliginosa* and proposed four species: *vulgaris, varia, magnifica* and *flava.*

The first, *vulgaris,* is described as having "Corpore albo; capite immaculato; dorso maculis fuscis transversis; lateribus, abdomineque rarioribus, vario."

The specimen on which this description was based was "Hospitatur in Museo Illustris. Com. Turriani Viennae". The Illustris. Com. Turrianus was, according to Daudin (1802: 281), the Count of Turn. I have never found any reference to the fate of his collection. As there is nothing to distinguish *vulgaris* from *fuliginosa,* it must be considered a strict synonym.

Amphisbaena flava, based on one of Seba's plates, is also indistinguishable from *fuliginosa* and hence represents another synonym.

Amphisbaena magnifica, also based on Seba, has as a difference a "taenia purpurascente supra oculos". This is no difference and so we have here another synonym of *fuliginosa.*

Amphisbaena varia, which has "corpore albo nigro, spadiceo, gryseoque vario" may be applied to the Colombian-Panamanian form, which agrees with this description as far as color pattern is concerned. Since no specimen is mentioned, nor any reference made to Seba, I present below a re-description and designate a neotype.

Gray (1844: 70) created a new name: *Amphisbaena americana*. This form is said to inhabit "South America, Berbice, Demerara" and for the time being doubtless should be regarded as a synonym of *A. f. fuliginosa*, to be revived in the event of the British Guianan population being recognized as a distinct form.

Amaral (1937) considered *Amphisbaena alba* as a subspecies of *fuliginosa*. As the two subspecies are sympatric everywhere between Baía and Trinidad, and no signs of polymorphism can be detected, there is no need of discussing this fantastic idea.

Since two names are available for the five subspecies here considered, three remain to be named. These I describe below as new.

Description of the subspecies of *A. fuliginosa*

AMPHISBAENA FULIGINOSA FULIGINOSA Linné, 1758

A. fuliginosa Linné, 1758: 229.
A. vulgaris Laurenti, 1768: 66.
A. magnifica Laurenti, 1768: 66.
A. flava Laurenti, 1768: 67.
A. americana Gray, 1844: 70.

Head massive; snout prominent, swollen. Body stocky, reaching a length of at least 420 mm. Tail cylindrical at the base, to the 6th–7th annulus, which is narrower than its neighbors, serving as a point for fractures. The truncated stump does not regenerate but heals perfectly. Distal segment of tail swollen.

Rostral moderate, low; nasals large, in contact with the second upper labial; prefrontals moderate; postfrontals together forming a rough hexagon, wider than long; occipitals variable; ocular irregular and extremely variable; eye usually visible; three upper labials, the first smallest, the second presenting frequent fusions and divisions that resemble pre- and anterior sub-oculars; one subocular, fairly constant, above the third upper labial, which may be split horizontally; two irregular temporal series; symphysial not always separated from the first lower labial, the suture being often incomplete in front; three or four lower labials, first fairly large, second often longitudinally split, the narrower part outside; one pair of chin-shields; post-symphysial elongate, sometimes split longitudinally, in contact or not with the first lower labial; shields following the chin-shields extremely variable.

Body annuli 196–213; tail annuli 24–28; segments to a midbody annulus 20–28/20–28; preanal pores 6–10; tail length at 400 mm body length variable within a very wide range.

Ground color yellow. Head immaculate or spotted; dorsal spots rather crowded, with distinct margins, tending toward a checkered pattern. Abdomen showing much less black than the dorsum.

Range. From Trinidad, where it intergrades with *A. f. varia,* to French Guiana. Intergradation to the south with *A. f. amazonica.*

Note. When identifying a specimen suspected of belonging to this race, use should be made of the various tables in the text, due to the heterogeneity of this form.

Type material. 1 sp. in Stockholm Museum; 1 sp. in Uppsala Univ.

AMPHISBAENA FULIGINOSA VARIA Laurenti, 1768

A. varia Laurenti, 1768: 66.

Scutellation agreeing with that of the typical form.

Body annuli 190–205; tail annuli 23–27; segments to a midbody annulus 20–26/20–26; preanal pores 6–9; tail length at 400 mm body length varying around 59.0 mm.

Ground color a dirty pinkish. Dorsal markings smudgy, very dense, almost obliterating the ground color. Abdomen as densely colored as dorsum.

Range. Panama and Colombia southward to near Villavicencio; southwestward to Ecuador and eastward to Venezuela near Trinidad. Intergradation with *amazonica, fuliginosa* and *bassleri.*

Type material.

Neotype MCZ 22070, ♂, from Barro Colorado Id., Panama, Canal Zone.

Paratypes

♂ ♂ MCZ 18924, 24004, 37874. USNM 38399.
♀ ♀ MCZ 18925, 24003, 37106, 37123. USNM 37859.
Not sexed BM 714.

AMPHISBAENA FULIGINOSA BASSLERI, subspec. nov.

Scutellation agreeing with that of the typical form.

Body annuli 204–215; tail annuli 26–30; segments to a midbody annulus 20–22/18–24; preanal pores 6–8; tail length at 400 mm body length varying around 67.5 mm.

Ground color yellowish. Head immaculate or spotted. Dorsal spots rarer than in any other form, with a tendency toward formation of narrow cross-bands. Abdomen usually nearly immaculate.

Range. Southern Peru and the Ucayali River valley up to the upper Amazon in Loreto. Intergradation with *varia* and *amazonica.*

Type material

Type AMNH 56606, ♂, from Roaboya, Loreto, Peru.

Paratypes

♂ ♂ AMNH 45624, 56590, 56594, 56597, 56599, 56603, 56607, 56608, 56610, 56613. CM 45472.

♀ ♀ AMNH 56310, 56588, 56589, 56592, 56596, 56598, 56601, 56602, 56605, 56609, 56611, 56617, 56618, 56660. CM 45471. MCZ 45784.

Not sexed BM 703, 704, 740, 744.

This form is named after the late Dr. Harvey Bassler, from whose splendid collection in the American Museum of Natural History almost all the material used in this description was obtained.

AMPHISBAENA FULIGINOSA AMAZONICA, subspec. nov.

Scutellation agreeing with that of the typical form.

Body annuli 207–221; tail annuli 24–27; segments to a midbody annulus 22–26/22–26; preanal pores 8–9; tail length at 400 mm body length varying around 50.0 mm.

Ground color yellowish. Head almost always immaculate; dorsal spots resembling the typical form; abdomen scarcely spotted.

Range. The Amazon valley from Manaus up to Leticia; possibly also the lower Amazon and northeastern Brasil. Intergradation with *bassleri, varia* and *fuliginosa;* possibly also with *wiedi.*

Type material

Type IB 674, ♀ from Manaus, Amazonas, Brasil.

Paratypes

♂ ♂ AMNH 64917; MCZ 19540, 20663, 20665.

♀ ♀ AMNH 64918, 64919; DZ 1927; IB 673; MCZ 20664.

AMPHISBAENA FULIGINOSA WIEDI, subspec. nov.

Scutellation agreeing with that of the typical form.

Body annuli 197–206; tail annuli 24–28; segments to a midbody annulus 26/24–26; preanal pores 8–10.

Ground color yellowish. Head immaculate or with very little spotting; dorsal spots very dense, almost completely obliterating the ground color; abdomen equally heavily colored.

Range. Known only from the type locality, Santa Maria, Baía, Brasil.

Type material

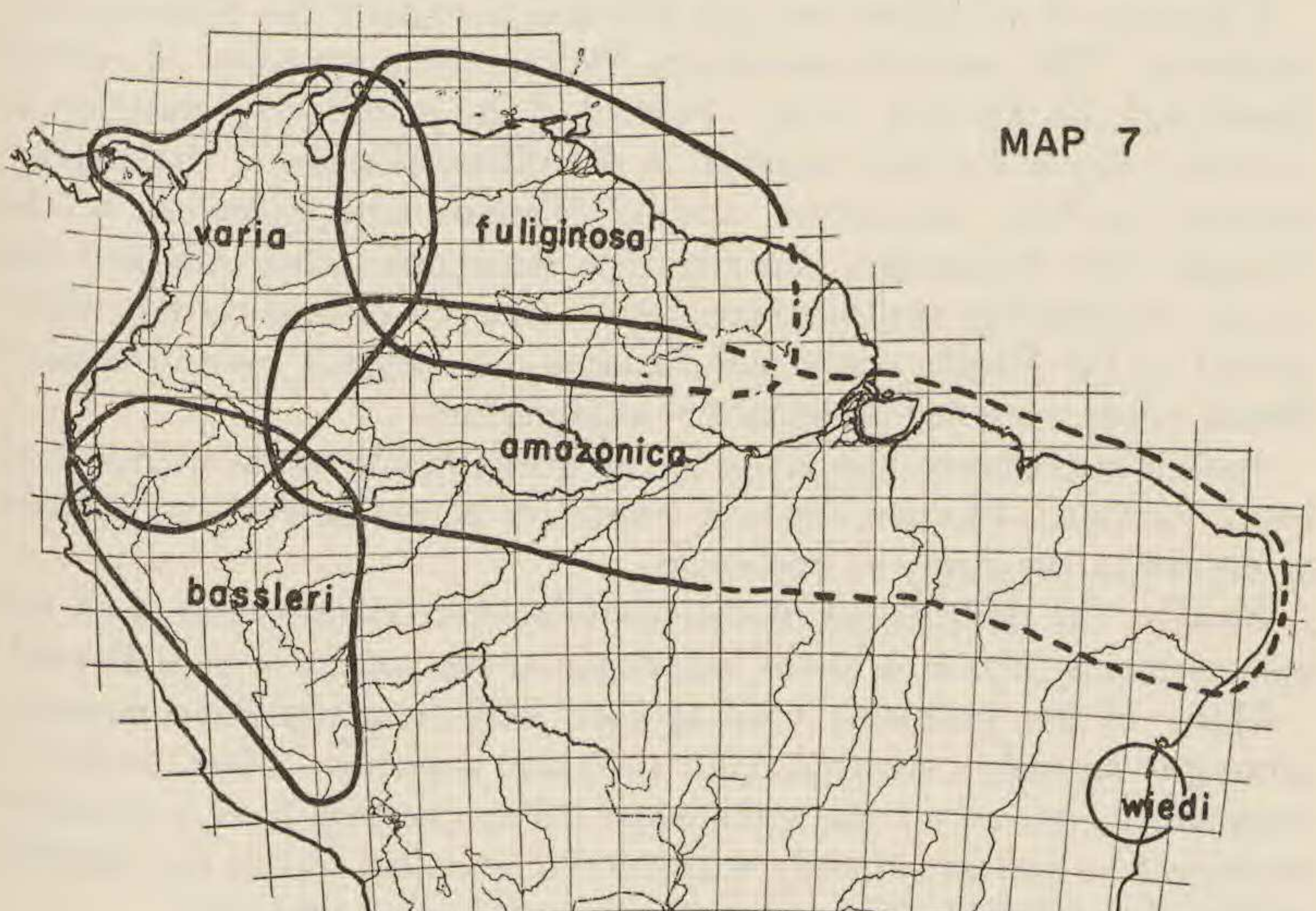
Type AMNH 1091, ♀.

Paratypes ♂ ♂ AMNH 1092, 1093.

SUMMARY

In this paper the distribution and differentiation of *Amphisbaena fuliginosa* are studied with the purpose of furnishing additional materials for the comparative study of patterns and mechanisms of evolution in natural populations.

One hundred and twenty-nine specimens were examined and 7 characters finally selected for statistical analysis: number of body annuli, number of tail annuli, number of segments to a midbody annulus (dorsal and ventral), number of preanal pores, relative tail length and color.



Map 7. *A. fuliginosa.* Tentative distribution of the races recognized in this paper.

The problem was first approached through a study of differentiation and intergradation of each character. For this purpose 9 basic samples were assembled; the criteria for their formation were the number of specimens available and the ecological homogeneity of the localities represented.

The results of this analysis were utilized for a study of the total likenesses and differences between the several samples, employing all the elements available.

From this study the conclusion was reached that five subspecies can be recognized in the territory covered. The recognition of these subspecies is a matter of convenience, since statistical differences between samples were found in all cases. Recognition was given only to those forms to which it is possible to ascribe a single individual or small sample with a reasonable degree of certainty. No arithmetical definition was attempted of this degree of certainty, but it is undoubtedly high in the forms considered. As a result of this policy one subspecies (*A. f. fuliginosa*) is based on somewhat heterogeneous material and it is to be expected that modifications of its status will follow the study of more abundant material.

A pattern of evolution was put forward to explain the observed distribution. This pattern postulates Pleistocene occupancy of central Brasil and the Amazon valley. Spread of the primitive population to northern South America resulted in the differentiation of three races: *bassleri*, in Peru, *amazonica*, around Manaus and *fuliginosa* in the Guianas and Venezuela. Finally, the Amazonic stock climbed the Andes, originating another race, *varia*, sharply differentiated, which spread to the Pacific coast and Panama. A disjunct race in eastern Brasil, *wiedi*, received no definitive explanation.

Special importance was given to the presentation of the evidence at hand, for this is thought the best course for herpetological systematics as an aid to the study of evolution.

Finally, the deficiencies of the material were pointed out, and the most pressing problems in the taxonomy of the species were indicated.

Many of the problems were treated only in a tentative manner, aiming to furnish a starting point to future research. I feel, however, reasonably sure about the systematic status presented, as it is rather conservative and has already withstood a practical test in the identification of the British Museum collection and other material.

ACKNOWLEDGMENTS

This study was made possible by the loans of material belonging to several institutions listed at the beginning of this paper. I am much indebted to their authorities, namely: Mr. C. M. Bogert and Mrs. B. M. Hecht at the American Museum of Natural History; Messrs. A. Loveridge and B. Shreve at the Museum of Comparative Zoölogy; Dr. K. P. Schmidt at the Chicago Natural History Museum; Dr. E. R. Dunn at the Academy of Natural Sciences of Philadelphia; Dr. Doris M. Cochran at the United States National Museum; Mr. J. R. Slevin at the California Academy of Sciences; Dr. G. S. Myers at the Museum

of Zoölogy at Stanford University; Mr. A. Hoge at the Instituto Butantan and Dr. H. W. Parker at the British Museum.

I am also very much indebted to Dr. A. S. Romer and Mr. A. Loveridge for the facilities necessary to accomplish this work and for many helpful suggestions.

During the preparation of this paper I received much help and encouragement from Dr. P. J. Darlington and Mr. C. M. Bogert, both of whom also read the manuscript. Also during the elaboration of this paper I had occasion to discuss repeatedly the problems here treated with Dr. Ernest E. Williams and Mr. Rodolfo Ruibal. None of these friends is, however, to be blamed for the shortcomings of this study.

LITERATURE

AMARAL, A.

1937. Estudos sobre Lacertilios Neotropicos. 4. Lista Remissiva dos Lacertilios do Brasil. Mem. Inst. Butantan **11**: 167–204.

BOULENGER, G. A.

1885. Catalogue of the lizards in the British Museum collections. **2**. London.

CARVALHO, A. C.

1946. Um novo genero de Ceratophrydideo do sudeste baiano. Bol. Mus. Nacional Rio de Janeiro **73**: 1–5.

COMRIE, L. J.

1944. Barlow's Tables. 4th ed. New York.

DAUDIN, F. M.

1802. Histoire naturelle générale et particulière des reptiles. **3**. Paris.

DUNN, E. R.

1931. The herpetological fauna of the Americas. Copeia 1931 (3): 106–119.

FISHER, R. A.

1948. Statistical methods for research workers. 10th ed. Edinburgh.

FISHER, R. A. and F. YATES

1949. Statistical tables for biological, agricultural and medical research. 3rd ed. New York.

GRAY, J. E.

1844. Catalogue of the Tortoises, Crocodilians and Amphisbaenians in the collection of the British Museum. London.

KLAUBER, L. M.

1938. A statistical study of the rattlesnakes. V. Head dimensions. Occ. Papers San Diego Soc. Nat. Hist. **4**: 1–53.

1941. Four papers on the applications of statistical methods to herpetological problems. I. The frequency distributions of certain herpetological variables. Bull. Zool. Soc. San Diego **17**: 1–31.

1941 a. Four papers on the applications of statistical methods to herpetological problems. IV. The rattlesnakes listed by Linnaeus in 1758. Bull. Zool. Soc. San Diego **17**: 81–95.

1943. Tail length differences in snakes with notes on sexual dimorphism and the coefficient of divergence. Bull. Zool. Soc. San Diego **18**: 1–60.

1943 a. A graphic method of showing relationship. Bull. Soc. San Diego **18**: 61–76.

LAURENTI, N.

1768. Specimen medicum exhibens Synopsin Reptilium . . . Vienna.

LINNÉ, C.v.

1749. Museum Adolpho-Fridericianum. Amoenitates Academicae **1** 11: 277–326.

1749 a. Surinamensia grilliana. Amoenitates Academicae **1** 16: 483–508.

1754. Museum S.M.R. Adolphi Friderici Regis . . . Holmiae.

1758. Systema Naturae. Ed. decima reformata. Holmiae.

MAYR, E.

1947. Systematics and the origin of species. 2nd print. New York.

MINER, J. R.

1947. Tables of $1 - r^2$ and $\sqrt{1 - r^2}$ for use in partial correlation and trigonometry. Photolithopr. reprod. ed. 1922. Baltimore.

MOOJEN, J.

1948. Speciation in the Brazilian spiny rats (Genus Proechimys, Family Echimyidae). Univ. Kansas Publ. Mus. Nat. Hist. **1** 18: 301–406.

SCHMIDT, K. P.

1936. Notes on Brazilian Amphisbaenians. Herpetologica **1**: 28–32.

SIMPSON, G. G.

1947. Tempo and Mode in Evolution. 2nd. print. New York.

SIMPSON, G. G. and A. ROE

1939. Quantitative Zoology. New York.

VANZOLINI, P. E.

1948. Notas sobre os ofidios e lagartos da Cachoeira de Emas, no Municipio de Pirassununga, Estado de S. Paulo. Rev. Bras. Biol. **8** (3): 377–400.

PLATE 1

Fig. 1. Linnean cotype of *A. f. fuliginosa* preserved at Stockholm. Kindness of Dr. U. Bergström.

PLATE 2

Fig. 2. *A. f. fuliginosa*. AMNH 8134. Paramaribo, Dutch Guiana.

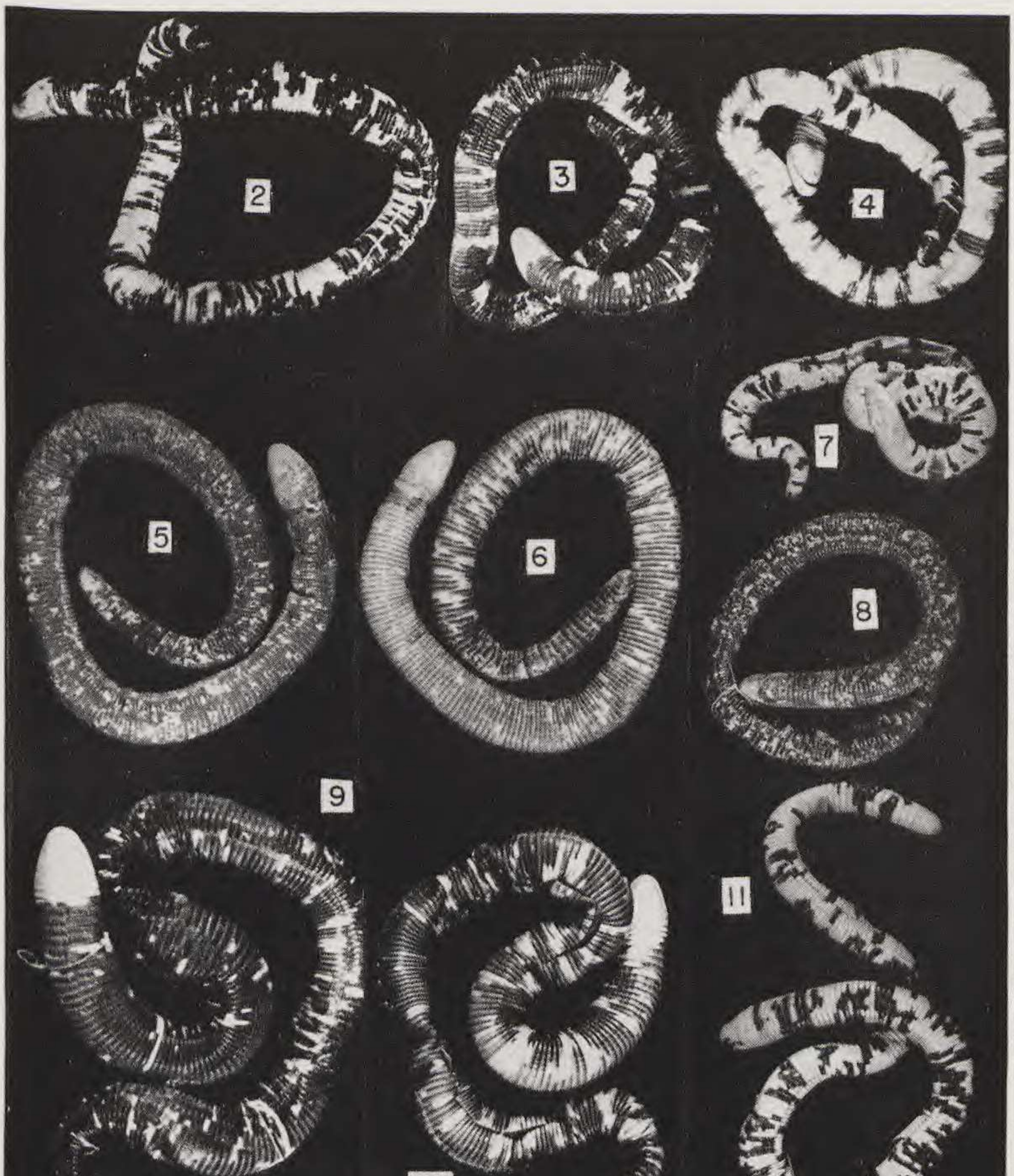
Figs. 3, 4. *A. f. amazonica*. IB 673. Manaus, Amazonas, Brasil. Type.

Figs. 5, 6. *A. f. varia*. MCZ 22070. Barro Colorado Id., Canal Zone, Panama. Neotype.

Figs. 7, 8. Intergrades between *A. f. varia* and *A. f. bassleri*. AMNH 2285 and 23326. Riobamba, Ecuador.

Figs. 9, 10. *A. f. wiedi*. AMNH 1091. Santa Maria, Baía, Brasil. Type.

Fig. 11. *A. f. bassleri*. AMNH 56606. Roaboya, Loreto, Peru. Type.


2
3
4
5
6
7
8
9
10
11